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FURTHER STUDIES OF INTERACTION BETWEEN PREDATORS AND PREY

BY G. F. GAUSE, N. P. SMARAGDOVA AND A. A. WITT

(Zoological Institute, Moscow University)

(With 6 Figures in the Text)

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1. INTRODUCTION

THE analysis of the numerical interaction that goes on generation after generation between a predator and its prey can undoubtedly throw much light upon the dynamics of animal populations. One of us (G. F. G.) has already summarised his experimental investigations of the subject (**3**, **4**). However, he felt that it would be desirable to confirm some of his conclusions by a more extensive experimental material, and that in other cases the collected data should be accounted for theoretically in greater detail. It is the object of the present paper to give the results of our further investigations carried out along these lines.

2. OBSERVATIONS ON THE INTERACTION BETWEEN TWO SPECIES OF MITES

(*a*) *Methods and previous investigations*

A mixed population of two species of mites, one of which, *Cheyletus eruditus*, feeds upon the other, *Aleuroglyphus agilis*, forms an excellent experimental material for the study of animal populations. The experiments were made in small open glass tubes containing 0·2 gm. of various nutritive substances.

The tubes were sterilised before inoculation with mites and kept in a moist chamber at 22° C. To prevent the mites crawling from one tube to another the tubes were kept in wide flasks containing 5 % KOH on the bottom. In addition, the rims of the flasks were covered with vaseline to prevent the mites from crawling over. The computation of the population was made at fixed intervals, and its technical details have already been described (**4**). Let us only note here that the contents of a culture was carefully mixed up with the aid of a thin needle, poured out on a glass plate, and divided into several equal parts (2, 4, 8, or 16). In two of such samples the total number of mites was counted (under a Zeiss binocular microscope), and then recalculated for the whole culture. After being counted, all animals were returned to the original culture. With such technique of counting we could separately keep the records for males, females, hexapod and octopod larvae; no attempt to count the total number of eggs was made in the present investigation.

The results of our previous experiments, made on wheat flour (**4**), can be summarised in the following four possibilities of interaction: (1) If we add a small number of predators to a dense population of the prey the predators cannot multiply and so perish. This is apparently due to the specific smell emanating from the prey. (2) If, however, we put the predators into a very sparse population of prey, the latter cannot be discovered and the predators will similarly perish—from starvation. An interaction takes place in the zone lying between these two extremes. (3) When the concentration of predators is considerable, they are able to devour the population of prey completely. The adults and large larvae of the prey are all devoured by predators. On small hexapod larvae and eggs, the attacks of the predators are much weaker and to a certain extent the prey escape destruction. The predators, when numerous, are in a position to devour the remaining prey as they get older. (4) But if the predators reach a fairly low concentration, they will not be able, after eating a large proportion of the prey, to destroy the remainder completely. The prey will begin to increase, this increase being in its turn followed by a new increase of the remaining predators. However, such periodic fluctuations in numbers are observed comparatively seldom in the absence of immigration from outside, and the interaction usually ceases, having followed type (3).

(*b*) *The effect of environment upon interaction*

Let us consider first how interaction between the two species depends on the properties of the environment. We have already remarked (**3**, **4**) that the *intensity* of consumption of one species by another may be peculiar for a given biological system. How far does this intensity depend upon the properties of the environment?

Fig. 1 represents three curves of interaction, each based on two independent experiments. They are given in a relative form, i.e. the concentrations of

predators (N_2) are placed on the abscissae, and those of the prey (N_1) on the ordinates. In the first case the environment consisted of 0·2 gm. of millet. The intensity of consumption was very high: the prey at once began to diminish in number and soon disappeared in the population. This was undoubtedly connected with the easy accessibility of the prey to the predatory mites on the firm surface of millet grains.

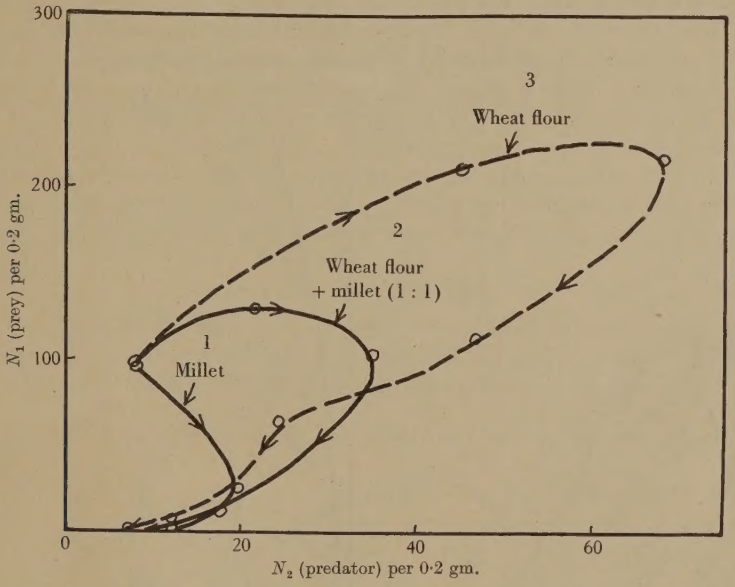

Fig. 1. Interaction between predators (*Cheyletus eruditus*) and prey (*Aleuroglyphus agilis*) on millet, wheat flour and a mixture of these substances.

Table 1. *Data on interaction between predators* (Cheyletus eruditus) *and prey* (Aleuroglyphus agilis) *on millet, wheat flour and a mixture of these substances*

	Millet		Wheat flour		Wheat flour + millet	
Days	Prey*	Predators*	Prey*	Predators*	Prey*	Predators*
1	100	8	100	8	100	8
8	92	8	131	11	—	—
19	24	20	236	68	100	36
26	—	12	60	24	12	12
36	—	—	5	12	1	5
43	—	—	3	12	—	2
50	—	—	—	1	—	—

* Total populations, including larvae and adults.

In wheat flour there is a greatly decreased intensity of consumption (curve 3). This decreased intensity, characterising the properties of the *whole* interacting system, finds its expression in a considerable initial increase of the

concentration of the prey. The efficiency of predators is less in the flour environment, and they check the multiplication of the prey only at a later stage of increase. The predators also partly die out before the final destruction of the prey, but this does not prevent the complete destruction of the latter. Curve 2, representing the interaction on the mixture of wheat flour and millet in equal quantities, is intermediate between 1 and 3. Original experimental figures can be found in Table 1.

The results of two extensive series of experiments are shown in Fig. 2. One was made on semoletta (a variety of semolina) (30 experiments) and

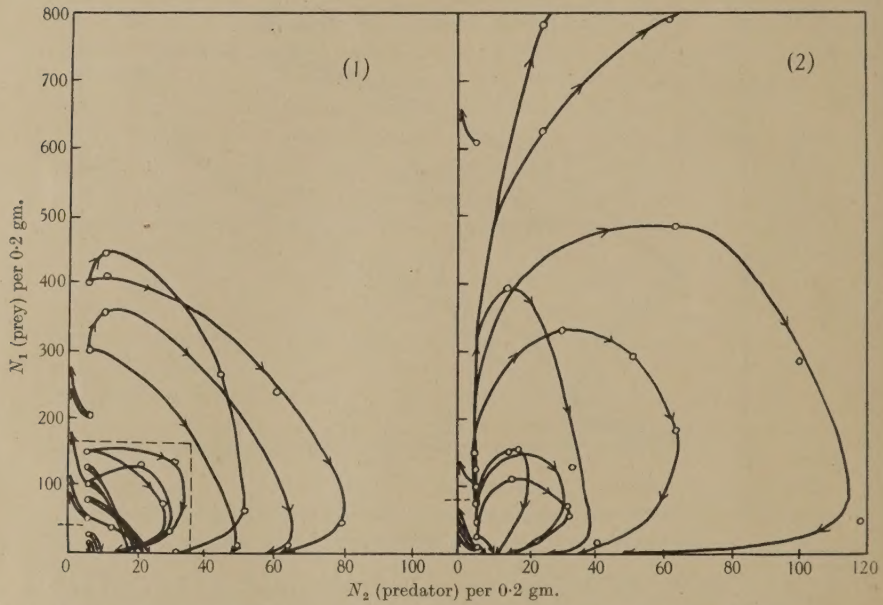

Fig. 2. Interaction between predators (*Cheyletus eruditus*) and prey (*Aleuroglyphus agilis*) on semoletta (1) and wheat flour (2).

another on wheat flour (18 experiments). It is evident that the interaction is more intense on semoletta where the prey is more accessible to the predatory mites. The set of curves reproduced on Fig. 2 (2) is obtained starting with initial concentrations of the prey not exceeding 150 per 0·2 gm., and is therefore comparable only with the lower group of semoletta curves, enclosed within the dotted lines on Fig. 2 (1).

Turning our attention to the interaction itself we find the following three possibilities of development: (1) Disappearance of predators with insufficient concentration of the prey. It is very distinct on the wheat flour in connection with difficulties in the search for prey, and is practically absent on semoletta.

(2) Interaction leading to complete destruction of the prey by predators. (3) Disappearance of predators in a dense population of the prey, which is more distinct on semoletta. Certain biological observations show that this line of development is a rather complicated one, and predators, which are unable to come into the dense population of the prey as a result of the smell emanating from the latter, may survive on the border of the culture and increase later when dying out from insufficiency of food has rarefied the population of prey.

From our previous observations we know that predators attack the small hexapod larvae of the prey less intensely than the older mites. It follows that the age distribution of the latter changes during the growth of the mixed culture. Fig. 3 (2) shows the data of one of the experiments in which at an early stage of growth, when the predator was not numerous, the prey population consisted of adults (10 %), octapod (40 %) and hexapod (50 %) larvae; before the final destruction of the prey its population consisted only of hexapod larvae.

(c) *The nature of interaction*

We may conclude that in the absence of immigration from outside, the interaction between the two species of mites does not produce regular periodic fluctuations in numbers, and forms a *relaxation interaction* (4). But when an

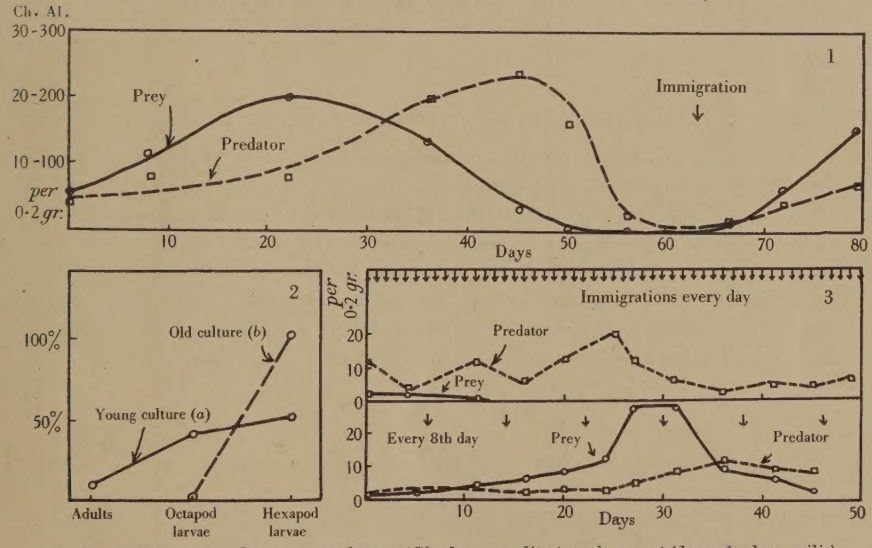

Fig. 3. (1) Interaction between predators (*Cheyletus eruditus*) and prey (*Aleuroglyphus agilis*) with an occasional immigration of the prey on the 63rd day. (2) Age distribution of the prey population (*a*) at an early stage of growth, and (*b*) before the final destruction of the prey. (3) Interaction between predators (*Cheyletus eruditus*) and prey (*Aleuroglyphus agilis*) with an artificial dosage of immigrations. All experiments refer to wheat flour.

occasional immigration is allowed, an oscillation immediately arises. Fig. 3 (1) presents the behaviour of the culture in which, soon after the destruction of the prey by predators (on the 63rd day), a few specimens of the former got access to the flour. This introduction caused a new cycle of multiplication of the prey and was followed by a new cycle in the growth of the not entirely extinct predator population.

Further experiments were made with artificially controlled immigration (Fig. 3 (3)). Two fertile females of the prey and two adult predators were added in the first group of experiments every day, and in the second every eighth day. In the first experiment these immigrations or "small impulses" were too frequent: the prey did not have an opportunity for development, and we ended up with a pure population of starving predators. In the second experiment with occasional immigrations we observed an oscillatory phenomenon of accumulation of the prey and its subsequent destruction by predators. This important problem of the frequency of immigrations and its role in the dynamics of fluctuations could perhaps be better elucidated by direct observations under field conditions.

(*d*) *Some tabular data*

It seems essential to publish original experimental figures, at least for some of our experiments, which might be used in the future for various other calculations. Table 2 gives some data on interaction between *Cheyletus* and *Aleuroglyphus* on semoletta and wheat flour.

3. Interaction between *Paramecium* and yeast cells

The technique of our previous investigations with this biological system has been described in (**3**) and (**4**). It can be summarised by stating that we cultivated Paramecia and yeast cells in glass tubes for centrifuging containing 5 c.c. of the liquid (Osterhout's medium as described in (**3**) buffered with the aid of 3 c.c. $m/20$ KH_2PO_4 per 100 c.c. and $m/20$ KOH to pH equal to 7·7). These tubes were shaken once a day to avoid the sedimentation of yeast, and kept in a thermostat with a glass wall at 23·5° C. Putting the general equation of interaction between predators (N_2) and prey (N_1) in the form

$$\left.\begin{aligned} \frac{dN_1}{dt} &= b_1N_1 - N_2f(N_1), \\ \frac{dN_2}{dt} &= kN_2f(N_1) - d_2N_2, \end{aligned}\right\} \qquad \text{.....(1)}$$

we can state that the multiplication of prey (yeast cells, *Saccharomyces exiguus*) per unit of time (b_1N_1) as well as the mortality of predators (*Paramecium bursaria*) per unit of time (d_2N_2) were maintained constant by addition of yeast cells and by rarifying Paramecia as described in (**3**) and (**4**), in order to measure the movement of the system due to the factors $N_2f(N_1)$ and $kN_2f(N_1)$.

Table 2. *Some data on interaction between predators* (Cheyletus eruditus) *and prey* (Aleuroglyphus agilis) *on semoletta and wheat flour. A fraction at the beginning of each experiment shows the initial relation between predators and prey; e.g.* 10/5 *means* 10 *prey and* 5 *predators*

	A. agilis					*Ch. eruditus*			
			Larvae				Larvae		
Days	♀	♂	6-pod	8-pod	Total	Imago	6-pod	8-pod	Total
					Wheat flour 10/5				
6	2	—	—	—	2	1	—	—	1
12	1	1	—	—	2	—	—	—	—
18	5	—	—	—	5	—	—	—	—
27	—	—	28	2	30	—	—	—	—
					Semoletta 10/5				
7	—	—	2	—	2	2	—	—	2
13	—	—	—	—	—	—	—	10	10
19	—	—	—	—	—	—	6	—	6
25	—	—	—	—	—	—	—	4	4
28	—	—	—	—	—	—	—	1	1
					Semoletta 10/5				
7	2	—	4	—	6	2	—	—	2
13	—	—	—	—	—	—	—	2	2
19	—	—	—	—	—	—	—	2	2
25	—	—	—	—	—	—	—	4	4
28	—	—	—	—	—	—	—	1	1
					Wheat flour 25/5				
6	—	—	1	2	3	—	—	—	—
12	6	3	1	7	17	1	1	—	2
18	12	6	10	8	36	—	2	2	4
23	2	4	24	12	42	2	—	—	2
27	8	—	188	8	204	8	—	—	8
32	—	—	104	—	104	—	16	—	16
35	16	—	24	32	72	—	16	16	32
38	—	—	—	—	—	—	8	16	24
41	—	—	4	—	4	8	4	—	12
47	—	—	—	—	—	—	—	4	4
					Semoletta 25/5				
7	—	—	10	10	20	2	—	—	2
13	6	4	18	22	50	2	—	—	2
20	8	2	10	12	32	2	14	6	22
24	—	—	8	—	8	4	—	8	12
30	2	—	6	—	8	2	2	4	8
33	—	—	—	—	—	6	—	—	6
36	—	—	—	—	—	—	1	—	1
					Wheat flour 25/5				
6	2	—	2	1	5	—	—	—	—
12	4	1	—	5	10	—	—	1	1
18	4	4	—	—	8	2	—	—	2
23	—	—	6	—	6	—	—	4	4
27	4	—	—	—	4	—	12	—	12
32	—	—	—	—	—	—	—	16	16
					Semoletta 25/5				
7	—	—	14	2	16	4	—	—	4
13	—	—	—	—	—	2	4	—	6
20	—	2	—	—	2	2	—	4	6
24	4	—	8	—	12	—	—	—	—
30	—	—	4	—	4	—	—	—	—
33	—	—	10	4	14	1	—	—	1
36	—	—	—	8	8	—	2	—	2
41	—	—	—	—	—	—	—	2	2

Table 2 (*cont.*).

	A. agilis					*Ch. eruditus*			
			Larvae				Larvae		
Days	♀	♂	6-pod	8-pod	Total	Imago	6-pod	8-pod	Total
				Wheat flour 50/5					
6	4	4	16	20	44	4	—	—	4
12	12	4	16	36	68	—	—	4	4
18	8	4	76	24	112	—	—	—	—
23	20	8	100	20	148	4	—	—	4
27	8	—	216	—	224	16	16	—	32
32	32	16	448	—	496	—	16	—	16
35	—	—	112	16	128	—	—	32	32
38	—	—	16	—	16	8	24	8	40
41	—	—	—	—	—	4	—	12	16
44	—	—	—	—	—	4	—	—	4
				Semoletta 50/5					
7	12	4	26	20	62	—	—	—	—
24	64	32	128	32	256	—	—	—	—
				Wheat flour 50/5					
6	—	—	12	12	24	4	—	—	4
12	20	8	—	—	28	4	—	8	12
23	12	8	228	8	256	8	—	4	12
27	24	16	32	336	408	8	16	—	24
32	32	16	336	112	496	—	64	—	64
35	80	16	160	32	288	48	16	32	96
38	8	—	16	8	32	32	56	32	120
41	—	—	—	—	—	8	28	8	44
44	—	—	20	—	20	12	8	4	24
47	—	—	—	—	—	4	—	4	8
				Wheat flour 75/5					
12	12	—	—	8	20	—	—	—	—
18	—	—	4	—	4	—	—	8	8
27	4	—	36	4	44	—	—	—	—
32	16	8	32	56	112	—	—	8	8
35	16	32	16	96	160	—	—	16	16
38	40	16	—	—	56	8	16	8	32
41	—	—	—	—	—	8	—	8	16
44	—	—	12	—	12	8	12	—	20
47	—	—	—	—	—	—	4	8	12
				Semoletta 100/5					
8	4	4	36	40	84	—	4	—	4
14	—	—	68	20	88	—	—	4	4
20	—	—	—	—	—	24	8	8	40
24	—	—	8	4	12	—	—	8	8
30	—	—	—	—	—	—	—	4	4
				Semoletta 125/5					
8	12	4	44	72	132	4	12	—	16
14	—	—	48	16	64	—	—	16	16
20	—	—	8	—	8	—	8	—	8
25	—	—	—	—	—	—	—	—	—
30	—	—	—	—	—	—	2	—	2
				Wheat flour 150/5					
7	12	4	24	64	104	—	—	—	—
13	24	24	88	88	224	—	—	8	8
19	64	40	72	112	288	8	8	—	16
24	8	8	160	56	232	16	—	—	16
29	64	24	184	64	336	—	24	8	32
33	—	—	192	—	192	32	32	—	64
36	—	—	16	—	16	—	4	12	16
38	—	—	8	—	8	4	16	20	40
41	—	—	—	—	—	8	—	8	16

To use a convenient expression of Chapman's (**2**), we arranged "synthetic populations". The consumption of prey by predators per unit of time $[N_2 f(N_1)]$ is given by the product of the concentration of predators (N_2) and specific consumption per predator per unit of time, depending on the concentration of the prey $[f(N_1)]$. The coefficient k in the second line of the equation (1) transforms the consumption of the prey per unit of time into an equivalent increase of the biomass of the predators.

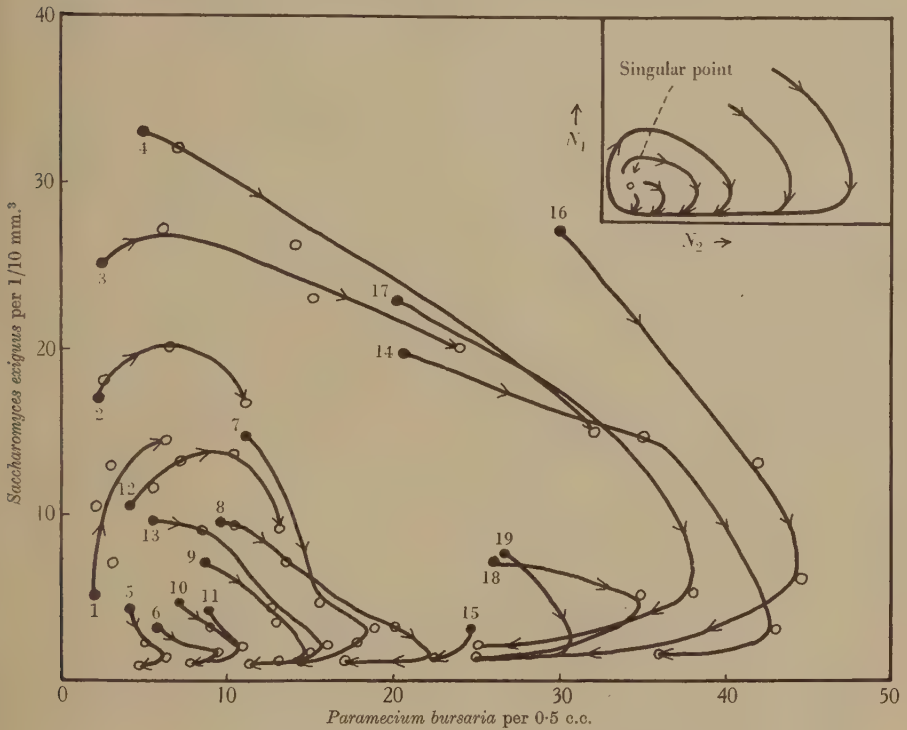

Fig. 4. Interaction between predators (*Paramecium bursaria*) and prey (*Saccharomyces exiguus*).

The conclusion of our previous investigations (**3**, **4**) was that, under the conditions as laid down above, periodic fluctuations are observed in the concentrations of both species. The *P. bursaria* cannot completely destroy the yeast cells and "sterilise" the microcosm, and at the same time do not disappear entirely from the population at the time of food shortage. We have also remarked (**3**) that these periodic fluctuations do not apparently belong to the "conservative" type. In other words they do not keep the magnitude initially given them but tend towards an inherent magnitude of their own. Let us continue here the analysis of this problem.

In our new experiments the coefficients of multiplication of yeast and of mortality of predators were correspondingly $b_1 = 0{\cdot}5$, $d_2 = 0{\cdot}4$. The only difference consisted in the following fact. In our previous investigations we made a definite initial combination between Paramecia and yeast cells and then followed the movement of the system for a relatively long time (17–25 days). In the experiments here described we simultaneously made 19 different initial combinations scattered on the graph N_1, N_2. Black circles on Fig. 4 represent these combinations 24 hours after the beginning of the experiment. They were followed for 4–7 days, and gave the direction of movement of the curves of interaction from various points, represented on Fig. 4. The advantage of this

Table 3. *Data on interaction between* Paramecium bursaria (*number of individuals per* 0·5 *c.c.*) *and* Saccharomyces exiguus (*number of individuals per* 0·1 *c.mm.*)

No. of exp.		Days						
		1st	2nd	3rd	4th	5th	6th	7th
1	*S.e.*	5	7	10·5	13	14·5	—	—
	P.b.	2	3	2	3	6·5	—	—
2	*S.e.*	17	18	20	16·5	—	—	—
	P.b.	2	2·5	6·5	11	—	—	—
3	*S.e.*	25	27	23	20	—	—	—
	P.b.	2·8	6	15	24	—	—	—
4	*S.e.*	33	32	26	—	15	—	—
	P.b.	5	7	14	—	32	—	—
5	*S.e.*	4	1·5	1·2	—	0·8	—	—
	P.b.	4	5	6	—	5	—	—
6	*S.e.*	3	1·5	1	—	—	—	—
	P.b.	5·5	9·2	6·5	—	—	—	—
7	*S.e.*	14·5	4·5	3·1	2·5	1	—	—
	P.b.	11	15·5	19	16	14·5	—	—
8	*S.e.*	9·5	7	3·2	1·5	1·5	—	—
	P.b.	9·5	13·5	20	22·5	16	—	—
9	*S.e.*	7	4	2·5	0·8	1	1·5	1
	P.b.	8·8	13	16	13·5	13	9	8
10	*S.e.*	4·5	3	2	1·5	1·5	1	—
	P.b.	7	9	9	10·5	9·5	7	—
11	*S.e.*	4	1·2	1	0·8	1	—	—
	P.b.	9	8·5	10	9	7	—	—
12	*S.e.*	10·5	11·5	13	14	9	—	—
	P.b.	3·5	5·5	7	10·2	12·5	—	—
13	*S.e.*	9·5	8	3·3	3·2	2	1·5	—
	P.b.	5·5	8	13	13·5	16	14·5	—
14	*S.e.*	19·6	14·5	3	2	2·5	—	—
	P.b.	20·5	35	43	36	22	—	—
15	*S.e.*	3	1	0·3	1·2	0·5	—	—
	P.b.	24·5	19	17	12·5	11	—	—
16	*S.e.*	27	13	6	1·5	—	—	—
	P.b.	30	42	44·5	27·5	—	—	—
17	*S.e.*	21·5	—	5	1·5	1	—	—
	P.b.	20	—	38	32·5	25·5	—	—
18	*S.e.*	7·5	5	2·1	0·8	1	—	—
	P.b.	26	35	32	20	17	—	—
19	*S.e.*	7·6	—	—	0·8	0·5	—	—
	P.b.	26·5	—	—	31	15	—	—

kind of experiment lies in the fact that they show us the behaviour of the system under environmental conditions which are all absolutely identical, except for the initial relations between N_1 and N_2. The corresponding numerical data can be found in Table 3.

It can be seen that a certain threshold concentration of yeast cells sedimenting on the bottom and elsewhere cannot be destroyed by predators; and predators, even under artificial rarification, do not seriously decrease in concentration until the destruction of the prey down to this threshold (which is partially connected with the decrease in the size of the predators). The threshold has in no way a firmly fixed value, but depends upon the concentration of yeast; when concentration is high, more cells sediment firmly on the bottom and escape destruction and the threshold is more pronounced. The escapes due to sedimentation and other causes, and consequently the threshold, intrinsically accompany the interaction between Paramecia and yeast cells.

When the concentration of Paramecia is low the yeast cells, with given rate of multiplication, increase in concentration; in this way the direction of our curves shows the character of periodic fluctuations, extending the picture previously obtained (**3**, **4**). It is interesting to note that a *stable* combination between *Paramecium* and yeast is impossible under the given conditions; the curves of interaction escape this combination. It follows that the "singular point" (for definition see below) is here unstable. The idealised curves of interaction are shown in the upper part of Fig. 4. It seems that in the case of mites the singular point is also unstable (see (**4**), p. 56). The closed circle reproduced there among idealised curves requires correction.

It would be interesting to account for the observed experimental situation theoretically. In accordance with our observations we can reproduce the function of the specific consumption per predator per unit of time $[f(N_1)]$ in the following form (Fig. 5 (1)): below a certain threshold r the prey (N_1) cannot be consumed. In the first approximation let us admit that near the threshold the function of consumption has a certain fixed value R; in other words, the search for food is very active. Turning to the equation (1) with $N_1 < r$ we obtain $dN_1/dt = b_1 N_1$ and $dN_2/dt = -d_2 N_2$, i.e. below the threshold the concentration of N_1 increases and that of N_2 decreases (Fig. 5 (1′)). With $N_1 = r$ the function $f(N_1) = R$; the condition $b_1 r - N_2 R = 0$ shows that with N_2 *exceeding* $N_2 = b_1 r/R$ the value $dN_1/dt = 0$. If the concentration of the predator (N_2) is below this point, the curve of interaction can rise from the threshold value (Fig. 5 (1′)).

It seems essential to give here a definition of "singular point", which may not be familiar to most readers of this *Journal*. Let the process under investigation be described by two differential equations of the first order:

$$\frac{dx}{dt} = P(x, y); \quad \frac{dy}{dt} = Q(x, y). \qquad \ldots\ldots(2)$$

These equations determine the movement of points $x(t)$, $y(t)$ representing various states of the system under investigation. Trajectories of these points on the surface x, y are integral curves of the equation

$$\frac{dy}{dx} = \frac{Q(x,y)}{P(x,y)}, \qquad \text{.....(3)}$$

Across every point on the surface x, y passes one and only one integral curve, with the exception of *singular points*, which satisfy the condition

$$P(x,y)=0;\ Q(x,y)=0. \qquad \text{.....(4)}$$

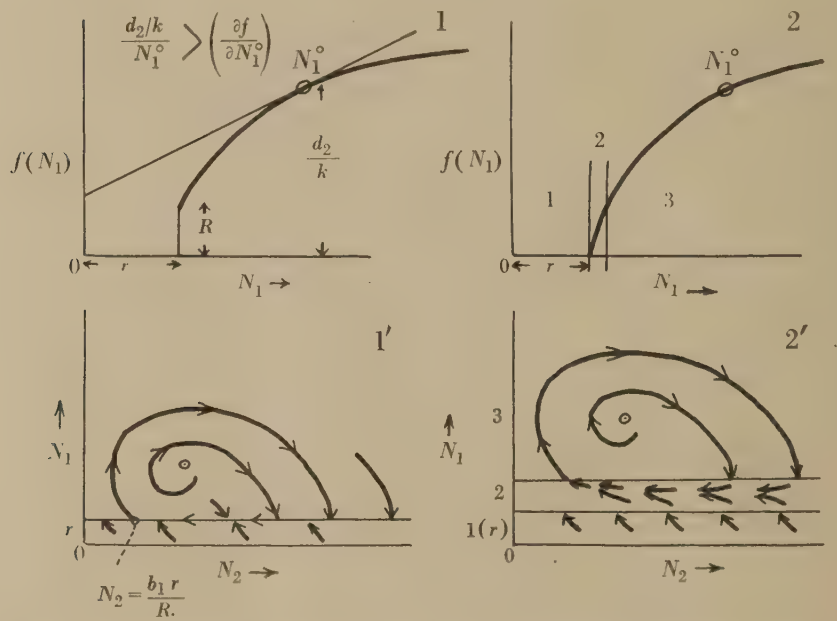

Fig. 5. Theoretical curves of interaction between *Paramecium bursaria* and *Saccharomyces exiguus*.

From (2) is seen that singular points of the equation (3) are *stationary states*, i.e. such states where for any t

$$\frac{dx}{dt}=0,\ \frac{dy}{dt}=0.$$

For examples of singular points see (5), p. 41.

Let us consider the singular point corresponding to the stationary state with positive N_1 and N_2 above the threshold. The condition of the stationary state is $dN_1/dt=0$ and $dN_2/dt=0$; or $f(N_1)=d_2/k$ and $b_1N_1-N_2d_2/k=0$. It follows that if $N_1>r$ the singular point will exist only if $R<d_2/k$. An analysis of the roots of "characteristic equation" shows that the singular point will

be *unstable* provided the tangent to $f(N_1)$ in the singular point crosses the ordinate and not the abscissa (Fig. 5 (1)).

The biological meaning of this requirement is not difficult to find: the instability of the singular point is a manifestation of the fact that *the variations of the specific consumption at the singular point feebly depend upon the variations in the concentration of* N_1. It is just what is to be expected for a biological system of this kind: the dependence between the two members of a food chain is not very "rigid". This point, however, requires further investigation.

The existence of the unstable singular point with the curves of interaction directed downwards on part of the territory, and the presence of a threshold zone with the curves directed upwards, is already a proof of the existence of a cycle of fluctuations analogous to those observed in the experiments (Fig. 5 (1′)). We can also add that our admission of the break of the function $f(N_1)$ at the threshold represents a special case of a sharp increase. In the case of the latter we shall have typical fluctuations with a "limiting cycle" (Fig. 5 (2, 2′)), and a little more the threshold concentration of yeast will be left out by Paramecia. If zone (2) is extraordinarily small, as perhaps it is, it will be difficult to make a choice between these two possibilities.

It seems reasonable to summarise the methodological essence of our mathematical calculations. We have, firstly, *observed* a specific kind of periodic fluctuation in the system of two interacting species. Quite independently of these fluctuations we have stated two biological peculiarities of our food chain: (1) the existence of threshold in the specific consumption of prey by predators, and (2) probable "non-rigidity" of their dependence. These two properties, formulated in a differential equation of interaction, lead to periodic fluctuations in numbers corresponding to those observed in the experiment. It is therefore probable that the *basic* features of interaction are in this way properly understood. At the same time room is open for further approximations and complications.

4. Interaction between *Paramecium* and *Didinium*

(*a*) *Mathematical expressions for interaction*

In this section we have already accumulated extensive experimental material (**3**, **4**), but there is need for adequate theoretical explanations. Experimental data on the interaction between *Paramecium caudatum* and *Didinium nasutum* described in (**3**) have shown that: (1) if the interaction has started it goes in only one direction—to the entire destruction of prey by predators; but if (2) the size of predators is small (starving individuals), and the concentration of predators and prey is low, the interaction may never start and predators will disappear.

Gause and Witt (**3**) tried to show in a general form that the oscillatory interaction assumed by Lotka and by Volterra is refuted by the following factors: (1) mortality of predators is practically non-existent up to the moment

of the entire destruction of the prey; and (2) the destruction of the prey (N_1) by predators (N_2) depends more on N_2 than on N_1. In better approximation to the actual state of affairs we assumed a slight mortality of predators when the latter are not numerous, which is responsible for their not starting at all in the population. However, for the sake of mathematical simplicity, we so simplified the situation that our theory was not free from empirical assumptions. We are therefore giving here a more complicated and rational theory of interaction, based on inherent biological properties of the system under investigation.

(*b*) *Variables*

Since in the process of interaction the size of prey does not change considerably, but that of predator can strongly decrease, modifying in this way the character of the interaction, let us introduce three variables as follows: (1) N_1, number of prey per unit of volume; (2) N_2, biomass (in volume units) of the predatory population per unit of volume; (3) n_2, biomass of a single predator. Then the number of predators will be given by N_2/n_2.

(*c*) *Equation of interaction*

The increase of the prey population is given by the difference of two factors, one of which depends on their multiplication $\left(bN_1 \frac{K-N_1}{K}\right)$ and another which represents the number devoured by the predator. This latter is given by the product of the number of predators (N_2/n_2) and specific consumption per single predator per unit of time, being a function of the size of the predator (n_2) and N_1: $f(n_2, N_1)$. Therefore

$$\frac{dN_1}{dt} = bN_1 \frac{K-N_1}{K} - \frac{N_2}{n_2} f(n_2, N_1). \qquad \text{.....(5)}$$

Alteration in the biomass of a single predator $\left(\frac{dn_2}{dt}\right)$ depends on two factors: (1) the factor of division, decreasing the size of the individual to half; and (2) the inflow of the nutritive substances from outside, compensating for the factor of division. The co-ordination of these two factors brings about the stable size of the cell.

The inflow of nutritive substances is evidently given by the specific consumption of the predator $f(n_2, N_1)$ per unit of time multiplied by a certain coefficient of proportionality k, reducing the *number* of consumed prey to the corresponding increase in *biomass* of the predator. In a first approximation this coefficient can be taken as constant.

The co-ordination of division with inflow is a problem of size regulation (1) and not of the interaction between species, and we do not intend to discuss it here in detail. Decrease in inflow of the nutritive substances usually brings a certain delay in division; but the rate of reproduction does not decrease so

strongly as the inflow, and the body size decreases accordingly. The factor of division may also be connected with the absolute size of the cell n_2. We put it in a general form $F(f(n_2, N_1), n_2)$, and therefore

$$dn_2/dt = -F(f(n_2, N_1), n_2) + kf(n_2, N_1) \quad \text{.....(6)}$$

The increase of biomass of predators (dN_2/dt) is given by the product of their number (N_2/n_2) and the increase of biomass of every individual due to consumption of the prey $kf(n_2, N_1)$. From this the mortality of predators has to be subtracted. This mortality occurs only among starving individuals and is therefore a function of n_2. We write

$$\frac{dN_2}{dt} = \frac{N_2}{n_2} kf(n_2, N_1) - f_1(n_2) N_2. \quad \text{.....(7)}$$

(*d*) *Properties of the specific consumption*

Fig. 6 (1) gives the observed relation between specific consumption of the predator per unit of time and the concentration of N_1 in normal (n_2 is about 0·9–1·0) and decreased starving (n_2 about 0·6–0·7) individuals. It is essential that with the least possible concentration of N_1 (one individual per 0·5–1 c.c.) the specific consumption has a finite value and then becomes zero with $N_1 = 0$. In order to decrease the concentration of N_1 we cannot break the individual and have to increase the volume of the environment. The necessity of prolonged search will enfeeble the predator and the situation will become more complicated. Here, as in the case of *Paramecium bursaria* and yeast, we admit that the form of function of the specific consumption at this stage cannot be further analysed. In *P. bursaria* no consumption is possible without the threshold residual; in *Didinium* a threshold is not inevitably included. These differences in the intensity of consumption are due to differences in the biological mode of nutrition.

Fig. 6 (2) is a half-schematical representation of the function of specific consumption, $f(n_2, N_1)$. To simplify the situation we do not take into account the influence of the concentration of predators upon their specific consumption. It is seen that if N_1 is low the starving predators have no consumption at all, and owing to their high mortality they disappear from the population before the concentration of the prey increases sufficiently.

(*e*) *The factor of division and function of mortality*

To simplify the problem of cell division, which is for us of secondary importance, we neglect the effect of n_2 and only consider the action of specific consumption alone. We admit also that $f(n_2, N_1)$ decreases, since in the case of increase we should take into account the phenomenon of hysteresis. Fig. 6 (3) schematically shows that with the decrease of inflow of nutritive substances (specific consumption) the rate of division also decreases, but to a smaller degree than the inflow. If, for instance, the specific consumption is

maximal (equal to 6) and $k = 0{\cdot}333$, it will give the $kf(n_2, N_1)$ equal to 2: the factor of division is also equal to 2, and the cell will not decrease in size. Low

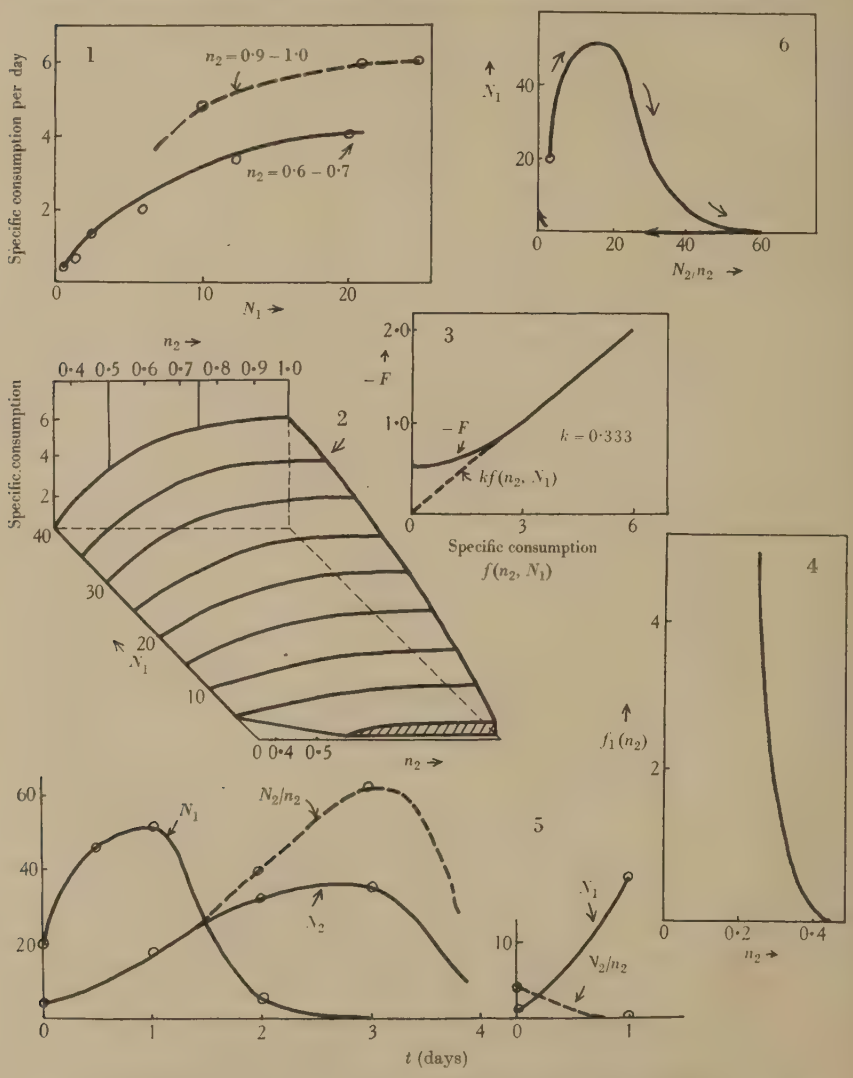

Fig. 6. Theoretical curves of interaction between *Paramecium caudatum* and *Didinium nasutum*.

consumption will not compensate for division; and with the inflow equal to zero the factor of division will still have a fixed value.

The function of mortality, reproduced on Fig. 6 (4), shows that for the individuals of the normal size the mortality equals zero. But when the insufficiency of food brings about decrease in size of the individual the mortality (starting with $n_2 = 0{\cdot}45$) becomes considerable.

(*f*) *The course of the relaxation*

When we put the values of functions reproduced on Fig. 6 into equations (5), (6) and (7), with the method of Runge-Kutta the course of interaction between the species can be easily calculated. The values of the coefficients b and K are taken from (**3**, p. 119). When we add 3 *Didinium* to 20 *Paramecium* (per 0·5 c.c.) the calculation will show complete destruction of the prey, decrease in size and dying out of the predators in accordance with the usual observations. These calculations are given on Fig. 6 (5). If we place a small predator ($n_2 = 0{\cdot}4$) with a single prey the former will disappear leaving a pure population of Paramecia (Fig. 6 (5)). Fig. 6 (6) represents these calculated results in a relative form; they perfectly agree with the results of observations previously described.

(*g*) *Conclusions*

Writing the equation of interaction between *Paramecium* and *Didinium*, based on experimentally observed biological properties of these species, we are led to relaxation of interaction between them. The predators can either not start at all in the population due to (1) practical impossibility of consumption of the prey for *small* starving predators when the concentration of N_1 is *low*, and (2) due to mortality of the small predators. Or, if the interaction has started, it will go in only one direction—up to the entire destruction of prey by predators due to: (1) the absence of mortality in non-decreased predators, and (2) the finite value of the specific consumption in *large* and *middle*-sized predators with the *minimal* concentration of the prey. In other words the consumption ability of common predators permits them to destroy the prey to the very end; but in small predators it is so insignificant that with the low concentration of the prey they disappear from the population entirely.

5. Summary

In this paper an account is given of our recent experimental and mathematical investigations on the nature of interaction between predators and prey, which have been carried out along three different lines.

Firstly, some new experimental data are presented dealing with a population of two species of mites, one of which, *Cheyletus eruditus*, feeds upon the other, *Aleuroglyphus agilis*. In these experiments an analysis is made of the effect of properties of the environment upon interaction by keeping the mites in various nutritive substances (wheat flour, millet, and semoletta). It is found that the predator is much more efficient in the open millet or semoletta

environment, where the prey is more available than in the wheat flour. Concerning the true nature of interaction, it is concluded that under the environmental conditions studied in this work the interaction between the two species of mites forms a *relaxation interaction*, so that periodic oscillations are prevented after one "cycle". But when an immigration is allowed such oscillations immediately arise. Some data are also given on age distribution and its variation in the course of the interaction.

Secondly, the classical case of relaxation interaction presented by two Infusoria, *Didinium nasutum* as predator and *Paramecium caudatum* as prey, is studied in detail from a mathematical viewpoint. An adequate differential equation of interaction between these two species based on experimentally observed biological properties of this system is formulated and leads to relaxation of interaction between them, which has been actually observed in our previous experimental investigations.

The third line of study is devoted to interaction between *Paramecium bursaria* and yeast cells, *Saccharomyces exiguus*. New experimental data are given showing, in accordance with previous observations, the possibility of continuous periodic fluctuations resulting from the very process of interaction between these two species. At the same time an impossibility of a stable combination between *Paramecium* and yeast cells is demonstrated and the curves of interaction are traced in detail. Independently of these fluctuations two biological peculiarities of the food chain under investigation are pointed out: the existence of a threshold value in the specific consumption of prey by predators (which is due to biological conditions of consumption), and the probable "non-rigidity" of their dependence. These two properties, formulated in a differential equation of interaction, lead to periodic fluctuations in numbers corresponding with those observed in the experiment. It is therefore probable that the basic features of interaction are in this way properly demonstrated.

REFERENCES

1. **Adolph, E. F. (1931).** "The regulation of size as illustrated in unicellular organisms." Baltimore.
2. **Chapman, R. N. (1934).** "An experimental analysis of the cause of population fluctuations." Science, 80: 297.
3. **Gause, G. F. (1934).** "The struggle for existence." Baltimore.
4. **Gause, G. F. (1935).** "Vérifications expérimentales de la théorie mathématique de la lutte pour la vie." Actualités Scientifiques et Industrielles, No. 277. Paris (Hermann and Co.).
5. **Lotka, A. J. (1934).** "Théorie analytique des associations biologiques. Part 1: Principes." Actualités Scientifiques et Industrielles, No. 187. Paris (Hermann and Co.).

EXPERIMENTS ON SOME FACTORS AFFECTING FERTILITY IN *TROGODERMA VERSICOLOR* CREUTZ. (COLEOPTERA, DERMESTIDAE)

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1. Introduction and acknowledgments

The results of some experiments carried out on the factors influencing fertility in several Phycitid moths of the genus *Ephestia* (Norris, 1933, 1934) caused the author to undertake a survey of the food requirements of adult Lepidoptera as a whole (Norris, 1934). Discussion of this problem indicated the existence in the family of a general evolutionary trend towards the total abolition of adult feeding, accompanied by progressive shortening of the adult life. The species of *Ephestia* concerned live in stored foods, and the flour moth, *Ephestia kühniella* Z., has reached such an advanced stage in the elimination of feeding that the adults are independent, not only of sugars, but also to a great extent of water. This species is consequently very well adapted to its life in flour mills where the usual sources of food and moisture are absent.

It is questionable whether *Ephestia kühniella* has adopted this specialised mode of life as a result of previous emancipation from adult feeding or whether the emancipation has been gradually evolved by a process of natural selection in the new habitat. This problem of "preadaptation" in relation to stored products insects has been discussed by Richards (1931).

It was observed that the Dermestid beetle *Trogoderma versicolor* Creutz., which, although it normally lives under the bark of trees, is also sometimes found infesting stored products, has a very short life as compared with other members of the same family such as the bacon beetle, *Dermestes lardarius* L. This observation led to the idea that a similar evolutionary trend may be at work in the Coleoptera as in the Lepidoptera, and a few experiments were made in order to see how far the biology of *Trogoderma versicolor* was comparable with that of *Ephestia kühniella*. Very little biological work appears to have been carried out with this beetle, although the better known Khapra beetle (*Trogoderma granarium* Ev.) has been studied by Voelkel (1924).

The work was carried out under the supervision of Prof. J. W. Munro, and I am indebted to Mr G. H. Mansbridge for providing cultures of the beetles for some of the experiments.

2. Materials and methods

Trogoderma versicolor has most often been recorded as infesting stored grain, but the source of the stocks used in the present experiments was a consignment of dried milk which had become infested in Spain. The beetles used

in the first two experiments were reared during larval life in ordinary glass jam-jars on a diet of flaked maize mixed with yeast meal. The mouths of the jars were covered with gauze and they were kept in an insectary which, as the time was summer, was unheated. The insects were removed from the cultures while in the pupal stage. The male pupae being on the whole smaller than the female ones it was possible to determine the sexes with fair accuracy.

The male and female pupae were put into separate boxes so that the newly emerged beetles were known to be virgins. All were then removed to a constant temperature of 27°C., there to await emergence of the adults. On emergence the males and females were isolated in pairs in corked tubes, 1 in. in diameter by 3 in. long. Before corking up the tube a plug of black tissue paper was placed in the mouth of the tube in order to prevent the beetles from laying their eggs in the crevices of the cork. This technique was indeed exactly similar to that employed in the experiments with *Ephestia* (Norris, 1933). The adults were kept at a temperature of 27°C. throughout life, and the eggs were counted as a rule every day, but were occasionally left for 2 days. From any one culture equal numbers of pairs were included in each part of the experiment.

3. Results

Experiment 1

42 pairs of newly emerged beetles were divided into 3 series of 14 each. The series were treated as follows:

A. Beetles kept in tubes containing a small quantity of yeast meal.
B. Beetles kept in tubes containing small squares of wet blotting paper.
C. Beetles kept in completely empty tubes.

Result

	A	B	C
Mean No. of eggs laid	122	122	129
Mean longevity of females (days)	11·3	11·6	10·5
Mean longevity of males (days)	18·6	20·8	18·7

It is evident from this result that the fecundity of the females (i.e. the number of eggs laid) is not increased by supplying them with food to eat or water to drink. Nor is their longevity increased by this treatment—the difference in mean longevity between the "B" and the "C" females not being statistically significant ($N = 26$: $t = 1{\cdot}79$: P lies between 0·1 and 0·05).[1] They are therefore independent of external sources of nourishment.

Experiment 2

It is usually considered that it is necessary for most beetles to pair repeatedly if they are to lay their full complement of fertilised eggs; Park (1933) demonstrated experimentally that this is the case in the flour beetle *Tribolium*

[1] The formula employed for testing the significance of differences between means is that given by Fisher (1928, p. 107).

confusum Duval. It was, however, suspected that in a short-lived insect such as *Trogoderma versicolor* one pairing might be sufficient, just as it is in the shorter lived Lepidoptera. The following experiment was carried out in order to test this point. The newly emerged beetles were divided into two series as follows:

A. The males were kept with the females throughout life.

B. The males were removed after the first batch of eggs had been laid.

Result

	A (20)	B (20)
Mean fecundity	97	95
Mean viability of eggs (%)	75·8	75·5
Mean longevity of females (days)	11·8	12·6
Total duration of the oviposition period (days)	5·8	6·2

The two series of beetles were thus completely comparable not only as regards mean fecundity and viability of the eggs but also, for all practical purposes, as regards the rate of oviposition. Repeated pairing is therefore unnecessary for the attainment of full potential fertility.

Experiment 3

Larvae of *T. versicolor* were reared on various foodstuffs and the fecundity of the beetles compared. It was unfortunately not convenient to test the viability of the eggs. The results of this experiment are not of any great theoretical importance and are recorded here without comment merely as facts which might possibly be of interest to a worker concerned in the rearing of the insects. Three series of cultures were set up on each of the following foodstuffs: oatmeal, wheat, wholemeal flour, maize. The cultures were made up in twelve jam-jars measuring approximately 2·5 in. in diameter, while the depth of the layer of food measured approximately 1·5 in. All were kept at a constant temperature of 27°C. 100 newly hatched larvae were put in each jar, and in any one series (i.e. set of four jars containing each type of food) the same number of offspring from any one pair of parents was put on each of the foods. The fecundity of ten pairs from each culture (i.e. 30 pairs from each foodstuff) was experimentally tested.

Result

Foodstuff	Mean fecundity
Wholemeal flour	104
Oatmeal	105
Maize	83
Wheat	67

The difference in mean fecundity between the beetles reared on maize and those reared on wholemeal flour was statistically significant ($N=58$; $t=3{\cdot}0345$: $P<0{\cdot}01$). Similarly the difference in mean fecundity between those reared on wheat and on maize is significant ($N=58$; $t=2{\cdot}5024$: P lies between 0·01 and 0·02).

These figures may be compared with those of Voelkel (1924) for *T. granarium*; at a temperature of 25° C. the females laid an average number of 65 eggs, the maximum being laid by any single female being 126. The beetles were reared either on wheat or on barley, but it is not clear which of these substances was used.

Concerning the time taken for development on the different foods at 27° C. the following details may be of interest. The newly hatched larvae were introduced into the cultures on August 18, 19, and 20.

	Flour	Oatmeal	Maize	Wheat
Date of emergence of first adult	Oct. 2	Oct. 8	Oct. 2	Oct. 3
No. of adults emerged before Nov. 2	245	208	205	208

4. Summary and conclusions

The biology of the stored products beetle *Trogoderma versicolor* Creutz. is quite comparable with that of the flour moth *Ephestia kühniella* Z., and it is consequently equally well adapted to life indoors. The similarity shows itself in the following ways:

(*a*) The life history is very short as compared with that of most other members of the same order and even of the same family.

(*b*) The beetles can be quickly and easily reared on a variety of foodstuffs at a high constant temperature. The rearing is not complicated by any tendency to diapause such as is found in many outdoor living insects.

(*c*) The adults require neither food nor water for the attainment of their full fecundity and longevity. In this respect they are even more specialised than *E. kühniella*, in which the fecundity and longevity are very slightly reduced if the adults are deprived of drinking water.

(*d*) Continued copulation throughout the oviposition period is unnecessary for the attainment of full potential fertility.

References

Fisher, R. A. (1928). "Statistical methods for research workers." London.

Norris, M. J. (1933). "Contributions towards the study of insect fertility. II. Experiments on the factors influencing fertility in *Ephestia kühniella* Z. (Lepidoptera, Phycitidae)." Proc. Zool. Soc. Lond. 903–34.

Norris, M. J. (1934). "Contributions towards the study of insect fertility. III. Adult nutrition, fecundity and longevity in the genus *Ephestia* (Lepidoptera, Phycitidae)." Proc. Zool. Soc. Lond. 333–60.

Park, T. (1933). "Studies in population physiology. II. Factors regulating initial growth of *Tribolium confusum* populations." J. Exp. Zool. 65: 17–42.

Richards, O. W. (1931). "Insects attacking stored products." Sci. Progr. Twent. Cent. 103: 474–85.

Voelkel, H. (1924). "Zur Biologie und Bekämpfung des Khaprakäfers, *Trogoderma granarium* Everts." Arb. Biol. Abt. (Anst.-Reichanst.) f. Land- und Forstwirtschaft, Berlin, 13: 129–71.

THE DISTRIBUTION OF ROCK POOL COPEPODA ACCORDING TO TIDAL LEVEL

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Hitherto the rock pool Copepods have been studied mainly from the systematic side: the present paper deals with some investigations into their ecology according to tidal level.

A series of pools ranging from low-water mark to well above high-water mark were chosen from amongst the saucer-shaped pools on "The Ledges" at Port St Mary, Isle of Man, figured by Knight and Parke (**3**). In all nine were chosen, and each had a number chipped out of the rock at the side to facilitate future identification, number 1 being the lowest of the series. The level and specific gravity of each was determined by Mr J. R. Bruce.

The Copepod content in April and August 1932 was determined by the following method. The whole of the water of the pool was siphoned through a length of hose pipe, and filtered through a silk plankton net, at the same time disturbing those Copepods which lurked amongst the weeds. When it was not possible to use the siphon, the water was baled through the net. Although some of the Copepods would have been left behind, the results are comparable. The figures were made comparable by calculating the number of Copepods per litre of each pool.

The volume of each pool was determined by refilling to the original level with known quantities of water. The hydrographical details and a description of the major fauna and flora of the various pools are given in Tables 1 and 2.

Pool 4, being out of the general sequence and chosen for another purpose, was not examined quantitatively for Copepoda and may therefore be omitted from the remainder of this paper. Pool 9 was the highest one on the shore and so at the upper limit of any possible series on the "Ledges". The last three pools, and especially the last two, dry up periodically and become salt cakes, while at other periods they are washed out by heavy rainfall, but are always more or less affected by splashes from high tides.

Table 1. *Hydrographical details. The tidal levels are given in feet above or below Ordnance Datum*

Pool no.	Tidal level	Specific gravity	Vol. in litres	Area in sq. ft.	General description of level
1	−1·33	1025·0	84	17	In the Fucoid zone but containing *Laminaria*
2	−0·47	1024·0	39	6	Upper Fucoid zone
3	+2·61	1027·7	7·5	3	Region of greatest number of *Patella*
4	4·91	1025·8	16	7	„ „ *Balanus*
5	4·78	1027·3	13·5	6	As Pool 4
6	7·53	1026·2	39	12	High-water mark
7	9·13	1026·6	84	18	1½ ft. above high-water mark
8	11·00	1026·4	9	5	3½ „ „
9	12·73	1010·5	36	8	5 „ „

Table 2. *The macrofauna and flora.* (*Flora determined by Dr M. W. Parke and fauna by Dr H. B. Moore*)

Pool 1.	*Laminaria:*	Wet weight (before rinsing)	1221 gm.	*Purpura*, 4
		Dry weight	211 gm.	*Sagartia*, 1
	Fucus:	Wet weight	3114 gm.	
		Dry weight	485 gm.	
Pool 2.	*Laminaria:*	Wet weight	113 gm.	*Patella*, 1
		Dry weight	17 gm.	*Purpura*, 11
	Fucus:	Wet weight	906 gm.	*Pomatoceros* present
		Dry weight	165 gm.	
Pool 3.	No *Laminaria* or *Fucus*; Coralline growth not determined			
	Patella, 46			*Purpura*, 1
	Balanus, 200			*Carcinus*, 1
	Littorina rudis, 1			*Collembola*, many
	Actinia, 7			
Pool 4.	No *Laminaria* or *Fucus*; Coralline growth not determined			
	Patella, 20			*Purpura*, 2
	Balanus, 3000			(?) *Spirorbis*, 2000
	L. rudis, 800			*Carcinus*, 6
Pool 5.	Coralline growth: Wet weight 1586 gm.			
	Dry weight 575 gm.			
	Patella, 21			(?) *Spirorbis*, 1000
	Balanus, 1500			*Carcinus*, 12
	L. rudis, 40			
Pool 6.	No Coralline growth:	*Chaetomorpha:* Wet weight	288 gm.	*Patella*, 1
		Dry weight	42 gm.	*L. rudis*, 200
		Ralfsia: Wet weight	120 gm.	
		Dry weight	30 gm.	
Pool 7.	*Cladophora* and *Chaetomorpha* (dead):	Wet weight	156 gm.	*L. rudis*, 100
		Dry weight	26 gm.	Many insect larvae
Pool 8.	*Enteromorpha* (bleached):	Wet weight	89 gm.	No macrofauna
		Dry weight	9 gm.	
Pool 9.	*Enteromorpha* (bleached):	Wet weight	107 gm.	No macrofauna
		Dry weight	17 gm.	

The rock pool Copepoda are very largely represented by Harpacticoida, and to a very small extent by Calanoida and free-living Cyclopoida. A summary of the chief species of Copepoda (all Harpacticoida) found in the eight pools during April 1932 is given in Tables 3 and 4. In pools 6–9 *Tigriopus fulvus* was the dominant species, representing 54, 92, 99·94 and 99·88 % of the whole. The small number of Copepods in Pool 7 may probably be explained by its large volume and lack of Algae giving a comparatively large amount of water where there are no weeds in which Copepods might lurk.

During August of the same year the pools were re-examined with special reference to *Tigriopus*. The numbers of Copepods had increased enormously

Table 3. *Numbers of species and individuals from the pools*

Pool no.	No. of species	No. of Copepods per litre
1	12	3
2	16	30·4
3	6	24
5	10	41·2
6	5	100
7	2	12·3
8	3	1769
9	2	807

Table 4. *The distribution of the more abundant species in the pools. The figures represent the numbers per litre in April* 1932

	1	2	3	5	6	7	8	9
Tigriopus fulvus (Fischer)	—	—	—	1	54	11	1768	806
Harpacticus gracilis Claus	0·7	7	10	2	—	—	—	—
H. littoralis Sars	0·5	4	—	—	—	—	—	—
H. uniremis Kröyer	—	3	—	—	—	—	—	—
H. flexus Brady	—	3	—	2	—	—	—	—
Dactylopusia brevicornis (Claus)	0·5	0·4	8	9	—	—	0·4	0·5
D. vulgaris Sars	0·5	5	2	2	4	—	—	—
D. thisboides (Claus)	—	0·8	—	—	—	—	—	—
D. neglecta Sars	—	1·5	—	—	—	—	—	-
Dactylopusia sp.*	0·4	3	—	2	—	—	—	—
Microthalestris forficula (Claus)	0·25	0·4	—	5·5	—	—	—	-
Idya furcata (Baird)	0·06	0·4	—	1	30·7	0·5	0·5	0·7
I. minor Scott	—	1	—	—	—	—	—	—
I. ensifera (Fischer)	0·06	—	2	—	—	—	—	—
Alteutha interrupta (Goodsir)	0·06	0·8	—	—	—	—	—	—
Amphiascus minutus (Claus)	0·06	—	2	—	4	—	—	—
Laophonte brevirostris (Claus)	0·06	0·8	—	3	—	—	—	—
L. strömi (Baird)	—	0·4	—	—	·	—	—	—
Ectinosoma gracile Scott	0·06	—	—	-	—	—	—	-

* *Dactylopusia* sp. = a species not identified with certainty, resembling *D. latipes* Sars, but not that species.

so that the upper pools were teeming with them. The quantitative results were: Pools 1–4, 0; Pool 5, 4; Pool 6, 1680; Pool 7, 2250; Pool 8, 8900; and Pool 9, 7800 per litre. It is amazing that these pools can maintain a population of 9 Copepods per cubic centimetre. A special investigation of the ecology and life history of *Tigriopus* from these pools was made, results of which have been published separately (**2**) and an experiment made to test the ability of *Tigriopus* and other forms from the upper pools to live in unaerated water (**1**). As Diatoms were not very abundant, the Copepods were probably feeding on the decaying *Enteromorpha*, in which case there would be abundant food for such numbers. It is probable that the upper two pools were supporting their maximum content, the limiting factor probably being oxygen.

Other pools in the vicinity, and also at Port Erin and Pooylvaaish, were examined qualitatively and their tidal levels noted. The results from these pools were compared with those from the first series. They confirm the fact that the greatest abundance of both species and numbers (apart from *Tigriopus fulvus* which is exceptional) occurs in the mid-tide or lower mid-tide levels.

The types most abundant at mid-tide level are the more typical Harpacticoids (Harpacticidae, Thalestridae, etc.) which are powerful swimmers. The pools from the upper levels commonly contain two species, *Idya furcata* and *Dactylopusia brevicornis*. Neither are powerful swimmers, *Idya furcata* is a common aquarium type and is capable of withstanding the environmental changes of an aquarium or upper tidal level pool.

The lower tidal level pools, containing *Laminaria* and red Algae, contain two types of Harpacticoida: (1) the typical form so abundant in the mid-tide

region, lurking amongst the smaller weeds, and (2) flattened forms living attached to the *Laminaria*. These flattened forms were never found in pools without *Laminaria*, although *Alteutha interrupta* was the only species represented in the series. This form, with *Zaus spinatus*, was abundant in the lower pools at Pooylvaaish and Port Erin. Also present there, but not so abundantly, was *Porcellidium fimbriatum*, an extremely flattened type. *Alteutha*, *Porcellidium* and *Zaus* can usually be found by lifting the *Laminaria* out of the water, when they can be seen running along the fronds with amazing rapidity. Although the fronds of *Laminaria* are the natural habitat, occasional specimens of *Alteutha interrupta* are found in pelagic plankton hauls. I have found it in plankton from the Clyde area, and a few times in the records from the "continuous plankton recorder" in regular use from Hull: in the vicinity of Borkum Light Vessel (one specimen), Cromer Light Vessel (one), Humber Light Vessel (two)—all in shallow water with a sandy bottom. *Zaus spinatus* were frequently seen in pairs, and in this form, as in *Tigriopus* (2), the female is usually at a late copepodid and not at the adult stage.

Table 5. *A list of Harpacticoida taken in the Isle of Man* 1932–4 *and their relative abundance according to tidal level*

Species	Where found	Low tide	Mid-tide	High tide
Ectinosoma gracile Scott	P. St M., Pv., P. E.	×	–	–
Amphiascus longirostris (Claus)	P. St M.	×	–	–
Alteutha interrupta (Goodsir)	P. St M., Pv.	×	–	–
Porcellidium fimbriatum Claus	Pv.	×	–	–
Zaus spinatus Goodsir	P. St M., Pv., P. E.	×	p	–
Harpacticus gracilis Claus	P. St M., Pv.	p	×	–
H. littoralis Sars	P. St M.	p	×	–
Idya ensifera (Fischer)	P. St M.	p	×	–
Microthalestris forficula (Claus)	P. St M., P. E.	p	×	–
M. littoralis Sars	P. St M.	p	×	–
Dactylopusia sp.	P. St M.	p	×	–
Amphiascus thalestroides Sars (?)	P. St M., Pv., P. E.	p	×	–
A. minutus (Claus)	P. St M.	p	×	p
Dactylopusia vulgaris Sars	P. St M.	p	×	p
D. brevicornis (Claus)	P. St M., P. E.	p	×	p
Ectinosoma gothiceps Giesbr.	P. St M.	–	×	–
Harpacticus uniremis Kröyer	P. St M., Pv.	–	×	–
H. flexus Brady	P. St M.	–	×	–
Idya minor Scott	P. St M., P. E.	–	×	–
Thalestris brunnea Sars	Pv.	–	×	–
T. longimana Claus	Pv.	–	×	–
Dactylopusia thisboides (Claus)	P. St M.	–	×	–
D. neglecta Sars	P. St M.	–	×	–
Westwoodia nobilis (Baird)	P. E.	–	×	–
W. pygmaea (Scott)	Pv., P. E.	–	×	–
W. minuta Claus	Pv.	–	×	–
Mesochra pygmaea (Claus)	P. St M.	–	×	–
Ameira minuta Boeck	Pv.	–	×	–
Laophonte cornuata Philippi	P. E.	–	×	–
L. similis (Claus)	P. E.	–	×	–
L. strömi (Baird)	P. St M.	–	×	–
Idya furcata (Baird)	P. St M., Pv., P. E.	p	p	×
Tigriopus fulvus (Fischer)	P. St M., P. E.	–	p	×

p = present.
× = region of greatest abundance.
– = not found.

P. St M. = Port St Mary.
Pv. = Pooylvaaish.
P. E. = Port Erin.

Photo. J. H. Fraser

Phot. 1. *Tigriopus fulvus*: an adult male clasping a 5th copepodid female (× 43).

Photo. J. H. Fraser

Phot. 2. *Porcellidium fimbriatum*: a flattened Harpacticoid inhabiting pools near low-water mark (× 52).

These flattened forms are recorded by Sars (**4**) as occurring down to 20 fathoms, and their absence in the upper pools is probably due to a definite correlation with tidal level. *Tigriopus*, too, is probably limited to the upper pools by a tidal level factor. Tidal and other physical conditions would prevent the occurrence of the typical mid-tide species in the upper pools, but there can be no serious limiting tidal factor in the lower pools as the typical species do occur there, some factor such as abundance or type of food making the mid-tide region more favourable for their existence (i.e. an indirect correlation with tidal level).

Of the Cylopoida and Calanoida, *Cyclopina gracilis* Claus, *Acartia discaudata* Giesbr., *Temora longicornis* (O.F.M.) and *Paracalanus parvus* (Claus) were taken from the oyster tanks at Port Erin, but were not found in the natural pools. Of the other Entomostraca, Ostracods were abundant, particularly at mid-tide level, and belonged to four species:

Cythere lutea O.F.M. Very common at mid-tide level (Pool 5) and present even above high-water mark (Pool 8). Port St Mary, Port Erin and Pooylvaaish.

Cythere albomaculata Baird. Distribution similar to *C. lutea* but not quite so common.

Paradoxostoma variabile (Baird). A few only, all mid-tide level. Port St Mary (Pool 5), Port Erin and Pooylvaaish.

Cytheridea punctillata (Brady). A few only from near Pat's Dub, Port Erin, mid-tide level.

Evadne nordmanni Lovén (Cladocera) was abundant in the oyster tanks at Port Erin but was not taken from the pools.

It is of interest to mention here the insect larvae found in Pool 7. These were *Chironomus* larvae, and although present in April 1932 were much more abundant in August, a quantitative analysis giving 155 larvae per litre, or 5 per square inch of bottom.

The identifications of Harpacticoida and Ostracoda were made from Sars (**4** and **5**). My thanks are due to Dr H. B. Moore for the collection of many of the pool samples, to Dr M. W. Parke, Dr H. B. Moore and Mr J. R. Bruce for their work in the analysis of the flora, fauna and physical conditions of the series of pools. The work was begun when I was Edward Forbes Exhibitioner, University of Liverpool, and continued at the University College of Hull.

SUMMARY

The tidal levels of a series of pools ranging from about low-water mark to beyond high-water mark were determined. The major flora and fauna of each was noted, and as far as possible all the Copepoda present were removed, identified and counted. This work was supplemented by a more general examination of other pools near this series and on other Manx shores. The most abundant Copepods living in rock pools are Harpacticoida. *Tigriopus fulvus* lives in pools at and above high-water mark and may reach a density of 9 per c.c. of water; but apart from this exception, the greatest number of both species and individuals occurs about mid-tide level. Flattened species

of Harpacticoida are found in the pools containing *Laminaria*, in which there are fewer typical forms. Rock-pool Ostracods, too, are most abundant at mid-tide level.

REFERENCES

1. **Fraser, J. H. (1935).** "An experiment on the powers of survival of animals and plants from a pool above high-water mark." J. Anim. Ecol. 4: 229–30.
2. **Fraser, J. H. (1936).** "The occurrence, ecology, and life history of *Tigriopus fulvus* (Fischer)." J. Mar. Biol. Ass. U.K. 20: 523–6.
3. **Knight, M.** and **Parke, M. W. (1931).** "Manx Algae." L.M.B.C. Memoir, vol. 30. Liverpool.
4. **Sars, G. O. (1911).** "An account of the Crustacea of Norway. 5: Copepoda, Harpacticoida." Bergen.
5. **Sars, G. O. (1928).** "An account of the Crustacea of Norway. 9: Ostracoda." Bergen.

AN INVESTIGATION OF THE PROFUNDAL AND SUBLITTORAL FAUNA OF WINDERMERE

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(*With 5 Figures in the Text*)

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1. Introduction

This paper contains an account of the qualitative and quantitative distribution of the macrofauna of the sublittoral and profundal regions of Windermere. The investigation extended over a period of 15 months, from January 1934 to March 1935.

2. Geology and physiography

Windermere, the largest of the English lakes, is situated in the southern part of the English Lake District. It is a long lake, lying in a deep trough-like valley, resulting from the deepening of a pre-Glacial valley during the Quaternary Ice Age. The lake basin is completely surrounded by siliceous Silurian and Ordovician rocks; only in the extreme northern end is there any limestone, represented by a small outcrop of Coniston Limestone. Windermere is served by a large watershed which covers approximately 90 square miles. The shoreline is undulating and well timbered. The lake is divided by a series of small islands into North and South basins. The investigation was confined to the North basin.

There are eleven large lakes in this district, all of which have the same trough-like appearance. Their original condition was rocky—the true oligo-

trophic character. With time this character changed in the various lakes according to the degree of wave action, fluvial deposition, and the nature of the surrounding land. Pearsall (**7**) has classified the north English lakes into two main types: Primitive and Evolved. Windermere belongs to the evolved or silted type: it is essentially an oligotrophic lake with certain eutrophic tendencies. The members of the phytoplankton vary between oligotrophic and eutrophic types at different seasons of the year. The onset of eutrophic conditions is indicated by the partially silted nature of the lake. The oligotrophic conditions present in Windermere are the steep shelving shore-line with a narrow littoral region, a trough-like shape, low salt concentration and the hypolimnion of greater volume than the epilimnion. The lake may therefore be regarded as an oligotrophic lake which is now in a transitional stage.

3. Apparatus and methods

Preliminary investigations in both the profundal and sublittoral zones were carried out, using a dredge designed by Beauchamp (**1**). The special feature of this dredge is the adjustable opening of the net and its sledge-like runners. Collections with this dredge were made between January 1934 and April 1934 at the following depths: 3, 6, 9, 12, 20, 30, 40, 50 and 60 m. This series follows the gradual increase in the distance from the shore. The 60 m. station was in about the middle of the lake. These preliminary dredgings showed a marked zonation in the macrofauna; but since these results were purely qualitative, another method to obtain quantitative results was adopted. For this purpose a Petersen Grab was used; but attempts to obtain satisfactory dredgings with it in the profundal region failed. For this reason particular attention was paid to the quantitative investigation of the sublittoral zone where the grab worked satisfactorily. Qualitative collections in the profundal were continued for the purposes of comparison.

Collections in the sublittoral were taken at 3–4, 6, 9, and 12 m. The 3–4 m. station depended largely on the presence or absence of plants at this depth. Collections were made as far as possible near plants, but not directly on them, as the Petersen Grab did not work satisfactorily over them. The following plants, however, have been brought up in the grab: *Isoetes lacustris*, *Littorella lacustris*, *Elodea canadensis*, and *Nitella opaca*. Three regions of the lake were selected: (1) Wray Bay, (2) Pullwyke Bay, (3) the "Congo", the latter being situated at the mouth of Blelham Beck. Particular attention was paid to (1) and (2), as they represented two physiographically different habitats. Wray Bay is exposed and the shore-line is comparatively unsilted, whereas Pullwyke Bay is reedy and has a highly silted shore-line. The "Congo" is approximately similar in physiographical features to Pullwyke Bay, and as there is little difference in the faunas, collections from the "Congo" were discontinued.

At each station four Petersen collections were taken. A complete collection consisted of the area covered and the volume of the mud brought up by four

Petersens. When working the grab it was noticed that the jaws closed slightly on entering the water. In order therefore to estimate the area covered, the area of a slightly closed Petersen was calculated by imprinting the edges of the jaws in the slightly closed position on a wet sample of mud. The average area between a partly closed Petersen and a completely open Petersen gave the approximate area covered by the grab. This area is 66 sq. in. (425·7 sq. cm.). Therefore the area covered by four Petersens amounted to 260 sq. in. (1702·8 sq. cm.). The volume of mud taken up by four Petersens was equal to 12 litres. All collections were put into buckets and sieved through a 2 mm. copper gauze sieve. The coarse residue was placed in bowls and taken to the laboratory where it was sorted and counted.

444 single Petersen dredgings were made in the course of this survey to estimate the density and zonation of the fauna. As each collection consisted of four Petersens, there were 111 collections altogether. In addition to these, collections were made for oxygen determinations, mud analysis, etc. At least 40 dredgings were also carried out in the sublittoral and profundal regions.

4. THE BOTTOM FAUNA

The bottom fauna is a typical mud fauna, the only groups found abundantly being *Pisidia*, Chironomidae (midges) and Oligochaeta (worms). The fauna in the sublittoral is supplemented by the additional groups of Ephemeroptera (mayflies), Trichoptera (caddis-flies), Neuroptera and Hydracarina (water mites). The fauna is not abundant, but as regards species it is comparatively rich. The numbers of species appearing on one or two occasions in collections is high. The fauna tends to be sporadic in the shallow sublittoral zone, but with increase in depth tends towards uniformity.

The sublittoral fauna may be conveniently divided into four main groups according to the degree of abundance of the species: *Common*, *Frequent*, *Rare*, *Very Rare*. Table 1 gives so far as possible all species found in the sublittoral and profundal zones. As the latter zone was only investigated qualitatively, the degree of abundance of the species in that region cannot be given in the same detailed way as for the sublittoral. *Common* forms are those forms which occur in over 60 % of the collections at 3, 6, 9 and 12 m. *Frequent* forms are those which occur in over 25 % of the collections. *Rare* forms are those which occur in less than 25 % of the collections. *Very Rare* forms are those which occur in less than 8 % of the collections. The specific distribution of the Tanypodinae and Tanytarsariae could not be attempted. Owing to the inadequacy of existing larval keys the separation of the larvae and their correlation with the hatched adult was quite impossible. The larvae are thus only represented by groups. An attempt was made to rear some of them in order to correlate larvae and adults. The majority of the larval types belonging to the Chironominae hatched successfully. The identification of the Oligochaeta is extremely difficult and is not complete. In some cases genera can only be

given, and as these may be represented by several species, too much attention should not be paid to their distribution.

Table 1

L. = a littoral migrant

Species	Sublittoral zone: Abundance	Sublittoral zone: Depth limit m.	Sublittoral zone: Remarks	Profundal zone: Abundance	Profundal zone: Depth limit m.	Profundal zone: Remarks
Platyhelminthes:						
Polycelis nigra (Ehrenb.)	V.R.	3	L.	—	—	—
Oligochaeta:						
Limnodrilus sp. (Claparède)	V.R.	3	L.	—	—	—
Eiseniella tetraedra (Say.)	R.	3	Usually associated with *Littorella* and *Isoetes* growths	—	—	—
Ophidonais sp. (Gervais)	F.	12	—	C.F.	20	—
Peloscolex ferox (Leidy)	—	—	—	C.	60	—
Hirudineae:						
Herpobdella atomaria (Carena)	F.	3	L.	—	—	—
Glossosiphonia complanata (Lin.)	R.	3	L.	—	—	—
G. heteroclita (Lin.)	R.	3	L.	—	—	—
Arthropoda:						
Asellus meridianus (Racovitza)	R.	3	L.	—	—	—
Gammarus pulex (Lin.)	F.	3	L.	—	—	—
Ephemoptera:						
Ephemera danica (Müll.)	F.R.	9	F. at 3 m., R. at 6 and 9 m.	—	—	—
Caenis sp. (Stephens)	C.F. R.	9	C. at 3 m. F. at 6 m. R. at 9 m.	—	—	—
Leptophlebia vespertina (Lin.)	F.	3	L.	—	—	—
Odonata:						
Agrion pulchellum (Lind.)	V.R.	3	L.	—	—	—
A. mercuriale (Charp.)	V.R.	3	L.	—	—	—
Neuroptera:						
Sialis lutaria (Lin.)	C.F.	12	C. at 3 and 6 m. F. at 9, 3, 12 m.	—	—	—
Trichoptera:						
Leptocerus aterrimus (Stephens)	C.F. R.	12	C. at 3 m. F. at 6 m. R. at 12 m.	—	—	—
Oecetis furva (Ramb.)	R.	9	—	—	—	—
Mystacides azurea (Lin.)	R.	6	—	—	—	—
Sericostoma personatum (Mc., Lach.)	R.	3	L.	—	—	—
Lepidostoma hirtum (Fab.)	R.	3	L.	—	—	—
Phryganea grandis (Lin.)	V.R.	3	L.		—	—
Diptera:						
Chaoborinae:						
Chaoborus plumicornis (Fab.)	R.	9–12	An overlapping species	C.	40	Reaches max. at 25 m.
Chironomidae:						
Ceratopogoninae:						
Ceratopogoninae *vermiformes* gr.	C.F. R.	12	C. at 3 and 6 m. F. at 9 m. R. at 12 m.	—	—	—
Tanypodinae:						
Trichotanypus (gr.)	C.	12	Represented by at least two species	C.	60	Well represented in profundal
Tanypus monilis (Lin.)	F.	6		—	—	
T. costalis (gr.)	—	—	—	R.	60	—

Table 1 (*cont.*)

Species	Sublittoral zone: Abundance	Sublittoral zone: Depth limit m.	Sublittoral zone: Remarks	Profundal zone: Abundance	Profundal zone: Depth limit m.	Profundal zone: Remarks
Chironominae:						
Chironomariae:						
Sectio C. genuinus:						
Chironomus cingulatus (Meig.)	C.F. R.	9	C. at 3 m. F. at 6 m. R. at 9 m.	—	—	—
Limnochironomus nervosus (Star.)	C.	6	—	—	—	—
Endochironomus albipennis (v. d. W.)	R.	6	—	—	—	—
Endochironomus sp. *Nymphoides* (gr.)	F.	12	—	F.	60	—
Sectio C. connectens:						
Polypedilum tritum (Wik.)	C.	12	—	R.	20	—
Microtendipes sp.	R.	9	—	—	—	—
Sergentia sp.	—	—	—	C.	60	Transitional type
Pseudochironomus prasinatus (Stgr.)	C.R.	9	C. at 3 and 6 m. R. at 9 m.	—	—	—
Stictochironomus rosenshöldi? (Zett.) (histrio gr.)	R.	9–12	An overlapping species	C.	40	Reaches max. at 25 m. Transitional type
Subsectio Cryptochironominae:						
Cryptochironomus sp.	F.	6	—	—	—	—
Tanytarsariae:						
Tanytarsus genuinus						
T. inermipes gr.	R.	12	—	—	—	—
T. Gregarius gr.	F.	12	—	F.	60	—
Orthocladiariae:						
Psectrocladius psilopterus (gr.)	R.	3	Particularly associated with *Littorella* growths	—	—	—
Heterotrissocladius sp.	R.	12	—	—	—	—
Monodiamesa bathyphila (Kieff.)	—	—	—	C.	15–20	Transitional type
Didiamesa sp.	R.	3	Usually associated with *Littorella* growths	—	—	—
Hydracarina:						
Limnesia maculata (Müll.)	F.R.	12	F. at 3 and 6 m. R. at 9 and 12 m.	—	—	—
L. undulata (Müll.)	R.	3	—	—	—	—
Dramenia crassipalpis (Sig Thor.)	F.R.	12	F. at 3 and 6 m. R. at 9 and 12 m.	—	—	—
Midea orbiculata (Müll.)	V.R.	3	—	—	—	—
Oxus strigatus (Müll.)	R.	6	—	—	—	—
Lebertia porosa (Sig Thor.)	V.R.	3	—	—	—	—
L. obscura (Sig Thor.)	V.R.	3	—	—	—	—
Hygrobates longipalpis (Herm.)	V.R.	9	—	—	—	—
Atractides anomalus (Koch)	V.R.	3	—	—	—	—
Piona coccinea (Koch)	V.R.	9–12	—	—	—	—
P. paucipora (Sig Thor.)	V.R.	12	—	—	—	—
P. longipalpis (Krend)	V.R.	9	—	—	—	—
P. rotundoides (Sig Thor.)	V.R.	3	—	—	—	—
Unionicola crassipes (Müll.)	V.R.	3	—	—	—	—
Forelia liliacea (Müll.)	V.R.	6	—	—	—	—
Diplodontus despiciens (Müll.)	V.R.	3	—	—	—	—
Arrhenurus crassicaudatus (Kran)	—	—	—	V.R.	20	—
A. nobilis (Neum.)	—	—	—	V.R.	20	—
Frontipoda musculus (Müll.)	V.R.	3	—	—	—	—

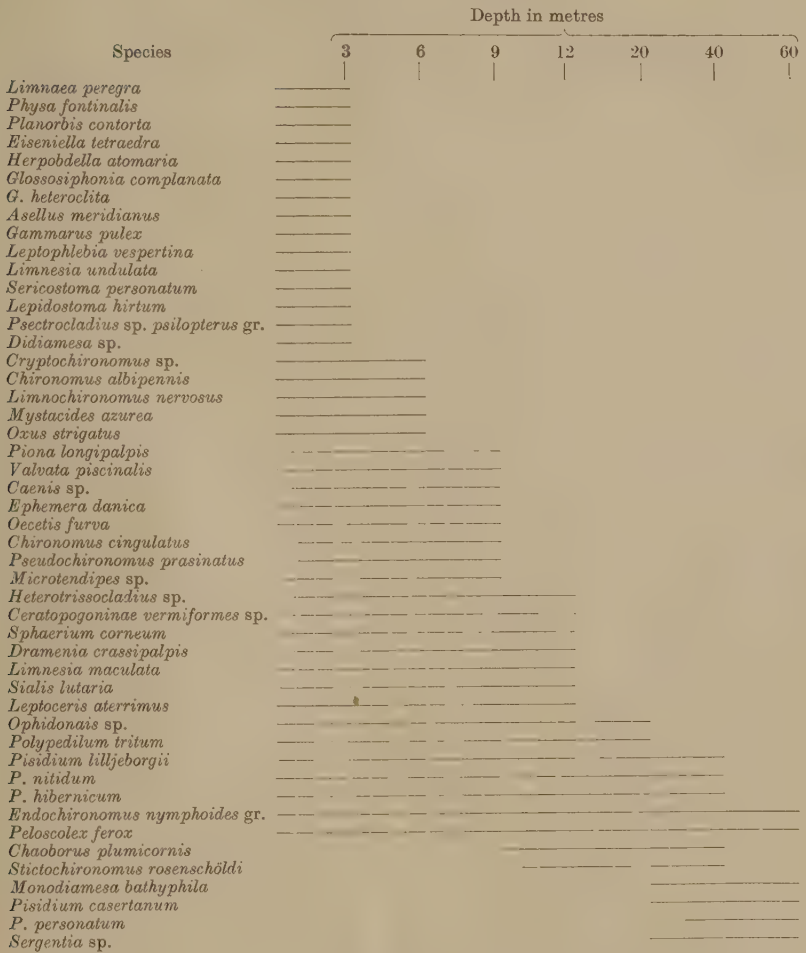
Table 1 (*cont.*)

Species	Sublittoral zone			Profundal zone		
	Abundance	Depth limit m.	Remarks	Abundance	Depth limit m.	Remarks
Mollusca:						
Sphaerium corneum (Lin.)	C.F.	12	C. at 3, 6, 9 m. F. at 12 m.	—	—	—
Pisidium lilljeborgii (Clessin)	C.F.	12	C. at 3 and 6 m. F. at 9 and 12 m.	F.	40	—
P. nitidum (Held.)	C. F. R.	12	C. at 3 m. F. at 6 and 9 m. R. at 12 m.	R.	30	—
P. hibernicum (Westerlund.)	F.R.	12	F. at 3 and 6 m. R. at 9 and 12 m.	R.	30	—
P. casertanum (Poli)	—	—	—	C.	30–60	True profundal type
P. personatum (Malm.)	—	—	—	C.	30–60	True profundal type
P. pulchellum (Jenyns)	V.R.	3	(L)	—	—	—
P. milium (Held)	V.R.	3	(L)	—	—	—
Limnaea peregra (Lin.)	R.	3	(L)	—	—	—
Physa fontinalis (Lin.)	F.	3	(L)	—	—	—
Planorbis contorta (Lin.)	F.	3	(L)	—	—	—
Valvata piscinalis (Müll.)	F.R.	9	F. at 3 and 6 m. R. at 9 m.	—	—	—

From Table 1 it can be seen that there is a definite zonation in the fauna, which may be divided into nine groups according to frequency at the various depths; but occasionally there are exceptions and a species may be found at a greater depth than is usual. These nine groups are: (1) Animals whose maximum depth range is 3 m. These may be termed *littoral migrants*, as most are known to occur on *Littorella* swards. Many of them come under the heading "Very Rare" in the foregoing table. (2) Maximum depth range 6 m. (3) Maximum 9 m. (4) Maximum 12 m. (5) Maximum 20 m. (6) Maximum 40 m. (7) Animals which are present only in the profundal zone, i.e. 12–60 m. (8) Animals present at all depths. (9) Animals which overlap between the sublittoral and profundal, i.e. present throughout the greater part of the profundal and in the deeper part of the sublittoral.

Table 2 summarises the distribution of the species in the sublittoral and profundal regions, the total number of species present being 48. The very rare species have been omitted as they are not important. From this table the number and percentages of species which belong to the various groups can be estimated. 73 % of the species are limited to the sublittoral zone. If to this 73 % are added the percentage of species belonging to groups 5, 6 and 8 it is found that 88 % of the total number of species occur in the sublittoral zone. This leaves only 12 % of the species which can be termed true profundal animals. The Tanytarsariae and Tanypodinae are not considered.

Table 2. *Depth distribution of the various animal groups in sublittoral and profundal zones*



5. THE IMPORTANCE OF THE PROFUNDAL FAUNA IN RELATION TO THE TRANSITIONAL CHARACTER OF THE LAKE

In the section geology and physiography mention was made of the transitional character of Windermere. Pearsall's (7) classification of Primitive and Evolved lakes is based on variations in the chemical composition of the various waters. The various stages of lake evolution are also reflected by the fauna,

particularly by those members of the fauna belonging to the Chironominae. This fact was originally pointed out by Thienemann (**11**), who classified fresh-water lakes into two main types. He drew attention to the fact that the oxygen content in the hypolimnion acts as a regulating factor, and in eutrophic lakes, where the deeper water is poor in oxygen during summer, the predominant forms are Chironomid species; while in oligotrophic lakes, where the deeper water is rich in oxygen in summer, the fauna is dominated by various *Tanytarsus* species. These lake types have been termed "Chironomus" and "Tanytarsus" lakes respectively. This classification remained unaltered for many years. However, as the study of limnology extended, and as more and more lakes were investigated ecologically, it appeared that many lakes differed faunistically from the two main types. Again, this variation is apparent particularly among the Chironominae. As a result of these more recent investigations, Lenz (**3**) has further classified lakes into four types. Types 1 and 4 are the same as those classified by Thienemann, while types 2 and 3 are transitional in character.

The four types, as defined by Lenz, are: (1) Tanytarsus lakes, (2) Stictochironomus lakes, (3) Sergentia lakes, (4) Chironomus lakes.

(1) This type of lake contains many *Tanytarsus* species, but *Lauterbornia coracina* is the dominant species. *Stictochironomus* species (histrio group) appears here also as the accompanying form. To this class belong the Weinfelder See and high Alpine lakes. This type of lake has been termed by Naumann ultra-oligotrophic.

(2) The Stictochironomus lake, as its name implies, is dominated by species of *Stictochironomus* (histrio group). The accompanying forms are various *Tanytarsus* species, *Sergentia* species, *Monodiamesa bathyphila* and *Didiamesa* species. To this type of lake most of the so-called Tanytarsus lakes conform, and include many oligotrophic lakes, such as the lower Lunzer See, Mond-See, Finnish lakes, the majority of the Norwegian lakes and the Polish Wigry-See.

(3) In this type *Sergentia* changes place with *Stictochironomus* species (histrio group), and becomes the dominant, while *Stictochironomus* is the chief accompanying form. *Tanytarsus*, *Orthocladian* and other *Chironomus* species are also present. An interesting characteristic of this type of lake is the presence of gill-less Chironomid forms only. This third class represents the boundary between the last stages of the oligotrophic and the first beginnings of the eutrophic condition.

(4) This is the Chironomus lake and represents true eutrophic conditions. The principal species found in this type of lake belong to the *plumosus* and *bathophilus* groups of the section *Chironomus genuinus*. The accompanying forms are *Microtendipes* and *Polypedilum* species. This fourth lake type stands in contrast to all others in that the accompanying forms are for the most part indicative of the sublittoral zone.

Monodiamesa bathyphila occurs in all types except in lakes where eutrophic

or oligotrophic conditions are extreme, while *Didiamesa* species are confined to lakes with oligotrophic tendencies. The distribution of the Tanypodidae is of no especial interest from the point of view of lake classification. They appear to be solely biocoenotic. That is, they are carnivorous and are only to be found in great numbers where suitable food is plentiful. The term "Tanypid Lake" is not therefore in use.

During the summer of 1935, I had occasion to study Chironomid systematics under the direction of Prof. Dr Thienemann and Prof. Dr Lenz at the Hydrobiologische Anstalt, Plön, Germany. I have compared the Windermere material with all the representative types of Dr Lenz' classification, and I am therefore in a position to classify Windermere with regard to its Chironomid fauna.

The Chironomid fauna of Windermere contains all the profundal types, which bear out the contention that Windermere is an oligotrophic lake, which is now in the process of evolution. How far this evolution has progressed can be roughly estimated by the species present and their relative abundance. Referring back to Table 1, it will be seen that the following species or forms, as the case may be, are present in the profundal zone: *Sergentia* species, *Stictochironomus* species (histrio group), *Monodiamesa bathyphila*, various *Eutanytarsus* forms, and one *Endochironomus* species (Nymphoides group). *Didiamesa* species is found in the sublittoral zone. Of the forms *Sergentia* is dominant, while *Stictochironomus* is also common; it is an *overlapping* form. The other accompanying forms are *Monodiamesa bathyphila*, *Eutanytarsus* species and a gill-less *Endochironomus* form. According to Lenz' classification therefore, Windermere belongs to the Sergentia Lake type. It thus represents a lake in the last stage of oligotrophism. The character of the sublittoral zone in Windermere indicates this fact even more definitely in this zone a gilled *Chironomus* form of the *bathophilus* group. *Chironomus cingulatus* is found, also *Polypedilum* and *Microtendipes* species, forms which are typical of a "Chironomus Lake" type. To sum up, therefore, Windermere may be defined as a Sergentia Lake with strong tendencies to eutrophic conditions in the sublittoral zone.

6. Density of the sublittoral fauna

The actual average density of the fauna has been calculated per square metre, as this makes results more comparable with other surveys. The density of the fauna of the sublittoral region is by no means high, but it shows a gradual decrease with increasing depth. The average number of animals per square metre at 12 m. is 5 % of that at 3 m. Nothing definite can be said regarding the density of the profundal, but information obtained from occasional collections at 15 and 20 m. seems to indicate that the fauna assumes a fairly uniform density, and there is no indication of the secondary maximum

which has often been noticed in other lake surveys, e.g. Lake Simcoe in North America (**10**).

The average number of animals per square metre is

3 m.	6 m.	9 m.	12 m.
550	230	100	30

This is the mean density; but it is important to understand that the fauna is subject to great seasonal variations.

Uniformity of the sublittoral fauna. The density of the sublittoral fauna on the whole tends to remain constant for any particular depth, but there is a tendency towards variation at 3 m. From Table 3 it can be seen that the average density at 3 m. in Wray Bay is much greater than the average density at 3 m. in Pullwyke Bay. If the figures for Wray Bay are taken as 100 % in each case and the figures for Pullwyke are expressed as a percentage of these, it is seen that whereas at 3 m. there is a divergence of 61 % between the faunas of the two localities, at 9 m. there is only 7 % divergence (see Table 4).

Table 3

Depth m.	Wray Bay No. of animals per sq. m.	Pullwyke Bay No. of animals per sq. m.
3	883	344
6	267	220
9	110	118
12	30	33

Table 4

Depth m.	Density in Pullwyke Bay relative to Wray Bay %	Percentage difference
3	39	61
6	82	18
9	107	7
12	110	10

It is reasonable to suppose from this that in the sublittoral there is a tendency towards uniformity and with increasing shallowness a tendency towards variation in the number of animals present. This difference in the density of the fauna at 3 m. in Wray Bay and Pullwyke Bay may possibly be accounted for by differences in their physiographical features. The littoral region of Pullwyke Bay is sheltered and muddy with a limited extent of stony substratum, while that of Wray Bay is exposed to wave action and the shoreline is free from mud and very stony. The possibility that these variations of the fauna might be due to a difference in the species present led to a comparison of the species in these two regions. The numbers of species present at 3 m. Wray Bay and Pullwyke Bay are 46 and 41 respectively. There is no significant difference in the species present in both regions. It is important

to note that the true sublittoral forms, i.e. those marked by C and F in the fauna table, are well represented in both localities. It is only the littoral migrants which differ, and these are of very little importance when the density is being considered. The density of the more important sublittoral animals at different depths is given in Table 5.

Table 5

Species	No. of animals per sq. m. in sublittoral zone at different depths			
	3 m.	6 m.	9 m.	12 m.
Caenis sp.	144	5	—	—
Pseudochironomus prasinatus	55	18	2	—
Pisidium lilljeborgii	48	48	21	6
Polypedilum tritum	45	24	10	4
Sphaerium corneum	39	15	10	2
Cryptochironomus sp.	33	1	—	—
Sialis lutaria	27	6	9	1
Valvata piscinalis	25	12	3	—
Chironomus cingulatus	22	10	—	—
Pisidium nitidum	19	4	3	—
Limnochironomus nervosus	18	8	—	—
Gammarus pulex	16	—	—	—
Herpobdella atomaria	12	—	—	—
Peloscolex ferox	12	3	10	1
Ephemera danica	9	—	—	—
Leptocerus aterrimus	9	3	3	—
Pisidium hibernicum	9	1	1	—
Ophidonais sp.	4	1	—	—
Planorbis contorta	4	—	—	—
Physa fontinalis	2	—	—	—

Fig. 1 shows the distribution of the various groups within the sublittoral. At all depths Chironomids outnumber all other groups, but this is most noticeable at 3 and 6 m. The Mollusca form with the Chironomids the principal members of the fauna. This condition is maintained to the deepest regions of the lake. The Ephemeroptera are important members of the fauna at 3 m., but they rapidly fall off in numbers with increase in depth. They do occur at 9 m., but their numbers at this depth are insignificant. "Others" include Hydracarina, Oligochaeta and Hirudineae, etc., whose individual numbers are too small to be shown graphically. The gradual decrease in numbers with increasing depth is shown by all groups.

Density of the Chironomidae in relation to one another. To show this the Chironomidae are subdivided into Ceratopogoninae, Tanypodinae, Tanytarsariae and Chironomariae. Their distribution in the sublittoral and their relation to one another are shown graphically in Fig. 2. The Chironomariae outnumber all others at 3 and 6 m.

Density of the Molluscan fauna in relation to one another. The group Mollusca is represented by seven common species. They belong to the Gastropoda and Sphaeriidae. Fig. 3 shows the relation of the *Pisidia* species, *Sphaerium corneum* and the Gastropoda to one another. The Sphaeriidae are the real

sublittoral representatives of the Mollusca, the two common species being *Pisidium lilljeborgii* and *Sphaerium corneum*. The Gastropoda are not at all

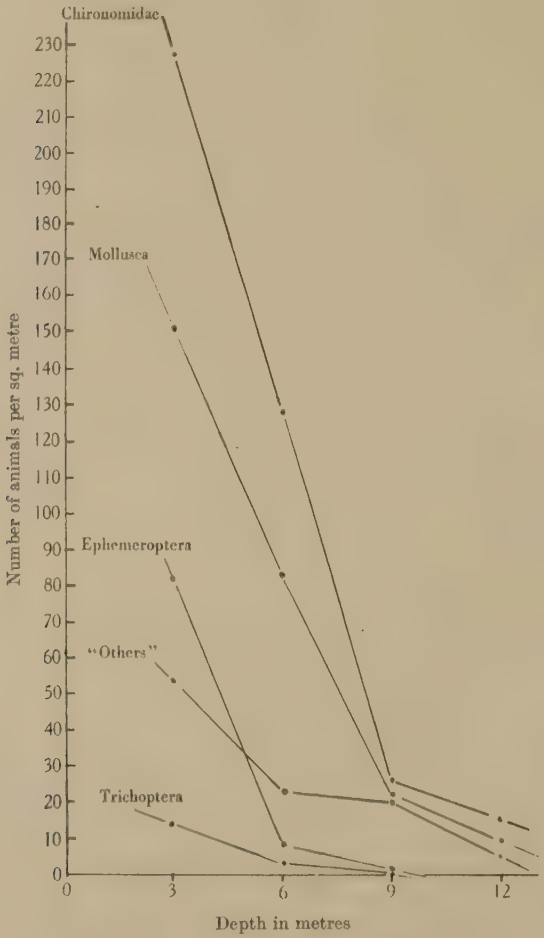


Fig. 1. Distribution of various groups within the sublittoral zone.

common except at 3 m. All except *Valvata piscinalis*, which occurs to a depth of 9 m., are littoral migrants.

Error of collecting. As the method of collecting is not accurate, an attempt has been made to estimate the error in the calculated density of the fauna.

The standard deviation of the numbers of the more common species has been estimated. This is expressed as the percentage standard deviation in Table 6.

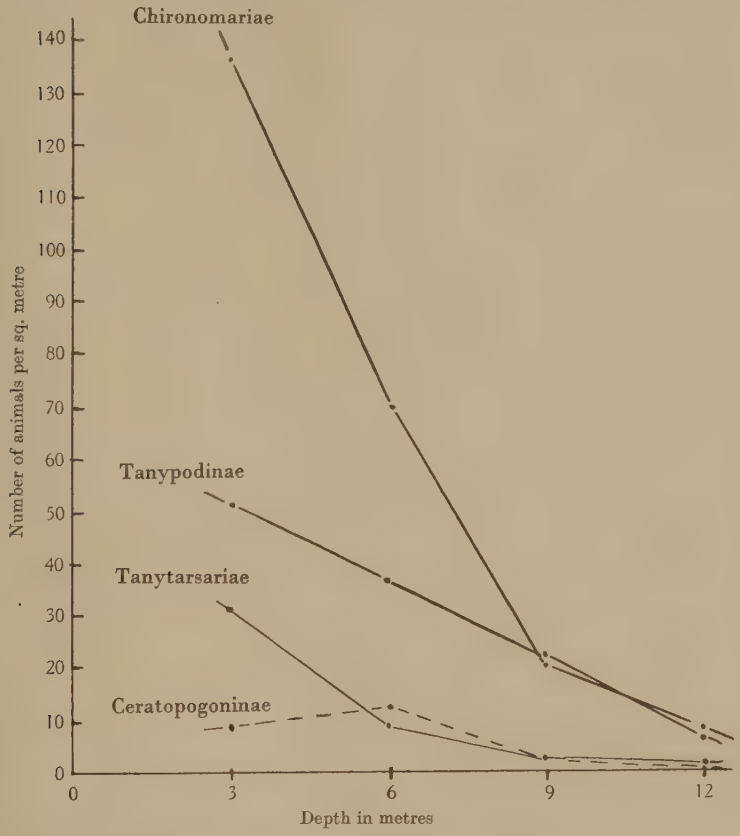


Fig. 2. Distribution of various members of the Chironomidae in the sublittoral.

Table 6

Species	Percentage standard deviation	Percentage error
Valvata piscinalis	178	118
Sphaerium corneum	210	140
Polypedilum tritum	67	44
Pseudochironomus prasinatus	62	41
Sialis lutaria	103	68
Pisidium lilljeborgii	115	76
P. nitidum	100	66

Mean error = 79 %

The percentage probable error has been estimated in each case by taking two-thirds of the standard deviation. The mean value of this is 79 %, and this is taken as the percentage error in collecting.

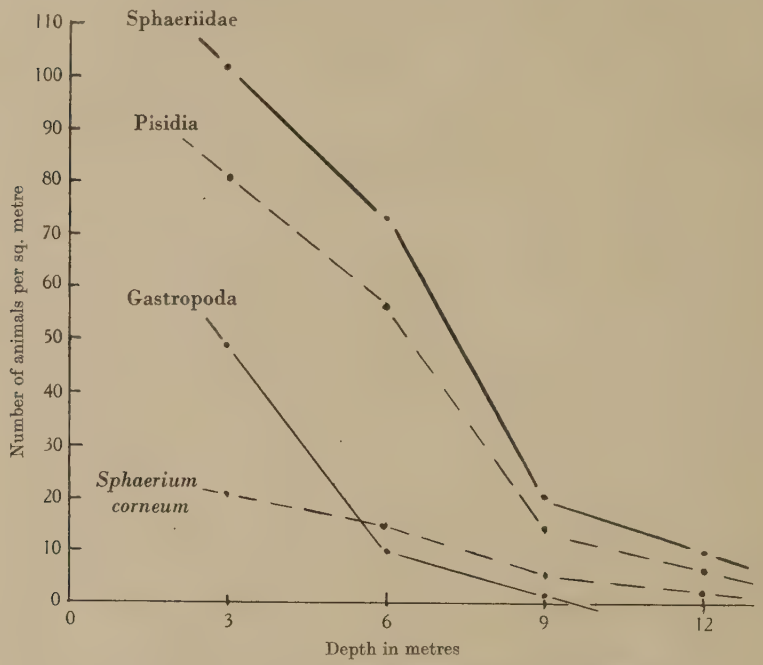


Fig. 3. Shows the distribution of the Molluscan fauna in the sublittoral.

7. Seasonal variation of the sublittoral fauna

The fauna of any lake may be divided into (1) a permanent fauna, (2) a temporary fauna. By permanent fauna is meant that part of the fauna which is present throughout the year. This group is represented by Molluscs, Hydracarina and Oligochaeta. By temporary fauna is meant that part which spends only a part of its life history in the water and whose presence is therefore seasonal. The members of this group are Chironomidae, Ephemeroptera and Trichoptera larvae. On account of this latter group the fauna of any lake will vary considerably with the seasons. Fig. 4 shows the mean distribution of these groups in the sublittoral zone. The figures are based on an average for all collections taken throughout the year. The average temporary fauna outnumbers the permanent fauna at 3 m.; but with increase in depth the two groups show convergence, so that each forms about 50 % of the fauna at 9 and 12 m. The great difference in the numbers of the two groups at 3 m.

is due to the large numbers of *Caenis* species, *Ephemera danica*, *Leptophlebia vespertina* and various Trichopterous larvae.

That the fauna is liable to great seasonal variations can be seen by comparing two collections taken at 6 m. in Wray Bay, one during the month of November when the fauna is at its maximum development, and the other in June when the fauna is at its minimum (Table 7). The seasonal variations of the temporary and permanent faunas have been plotted separately (Fig. 5). The seasons represented are winter, spring and summer. The seasonal variations of the temporary fauna are well marked. The temporary fauna is most numerous in the winter, and gradually declines until it reaches a minimum in the summer. The permanent fauna is also subject to seasonal fluctuations which are not, however, so well marked as in the temporary fauna. The greatest variation is between the winter and spring values. The winter maximum

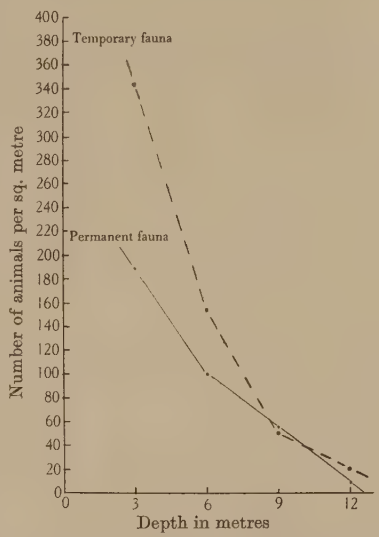


Fig. 4. Mean distribution of the temporary and permanent faunas in the sublittoral.

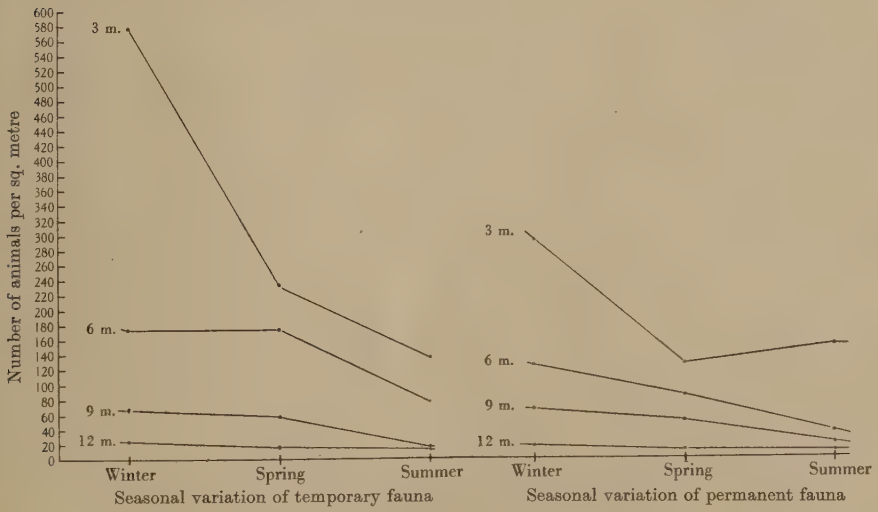


Fig. 5.

is due in part to the sudden increase in the numbers of very young Molluscs and Amphipods during the latter part of October and beginning of November. These individuals, owing to the method of collection, do not come under observation until they are over 2 mm. in size. Why the permanent fauna decreases in spring is difficult to explain, but it may quite possibly be due to the increased rate at which the fish feed at this time of the year.

Table 7. *Maximum and minimum densities at 6 m. in Wray Bay*

Species	November No. of animals per sq. m.	June No. of animals per sq. m.
Limnesia maculata	12	—
Oxus strigatus	—	6
Sialis lutaria	6	12
Ceratopogoninae vermiformes sp.	42	12
Tanypus sp.	78	—
Limnochironomus nervosus	12	18
Polypedilum tritum	60	—
Cryptochironomus sp.	6	—
Chironomus cingulatus	6	12
Pseudochironomus prasinatus	48	—
Leptocerus aterrimus	6	6
Ophidonais sp.	6	—
Peloscolex ferox	—	6
Pisidium lilljeborgii	54	12
Valvata piscinalis	18	18
Ephemera danica	—	6
Total	354	108

The seasonal variations in the temporary fauna are of interest. The winter and spring values in Fig. 5 show that there is a rapid fall in the numbers of the temporary fauna at 3 m. in spring, while at 6, 9 and 12 m. there is little change. A consideration of the spring and summer values shows that the decrease in numbers at 3 m. continues, but that a decrease has now also occurred at 6 and 9 m. The decreases are due mainly to the emergence of the adult animals. This delayed emergence of the deeper species may possibly be due to the lower temperatures of the water at these depths.

8. Layering of the animals in relation to the bottom deposits

The mud of the sublittoral zone is fine and generally uniform in character. But between 3 and 4 m. there is sometimes a change in uniformity, the substratum may become gritty and sandy. This is particularly the case where the neighbouring plant zone is dominated by growths of *Littorella* and *Isoetes*. As the Petersen Grab does not work satisfactorily over plant growths, this substratum hardly comes into consideration in this survey. However, it may influence the distribution of the littoral migrants whose habits are burrowing. A typical example of this is *Eiseniella tetraedra* which is only found in the gritty substratum. At 6 m. in Wray Bay the substratum shows a deviation from the general uniformity. Running across the bay at this depth is a layer of clay which shades from grey to green and is of a very sticky nature.

The mud may be divided into three layers: (*a*) A thin upper layer of newly deposited material which has a very characteristic brown colour. This layer represents the contact layer described by Lundbeck (**5**) and contains small reddish brown masses, diatoms and a few faecal pellets. (*b*) A thick grey layer which occupies almost one-third of the volume of the mud taken up by the grab. It contains many faecal pellets and Diatoms. The presence of these faecal pellets suggests that animal life may be most abundant here. (*c*) A yellow layer comprising the remaining mud brought up by the grab which contains fewer faecal pellets and exceedingly few Diatoms. The appearance is more homogeneous than in the other two layers. The clay at 6 m. in Wray Bay is similar to the sample described above except that the second layer consists of a sticky clay. This layer contains very few Diatoms and faecal pellets, which suggests that animal life in this region is confined to the contact layer.

Several collections were made for the purpose of determining the position of the animals in relation to this layering. The grab was opened carefully on to a board so that the contents came out *in situ*. The two topmost layers were scooped off with a glass plate and the contents sieved. The bottom layer was sieved separately. Collections were made at 4, 6, 9 and 12 m. in Wray Bay during the month of February. The results are shown in Table 8.

Table 8. *Position of the animals in relation to the layering of the mud*

	4 m.		6 m.		9 m.		12 m.	
Species	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom
Hydracnids sp.	1	—	2	—	1	—	—	—
Sialis lutaria	1	—	1	—	—	—	—	—
Ceratopogoninae vermiformes sp.	2	—	5	—	1	—	—	—
Tanypus sp.	26	9	3	1	5	—	1	—
Chironomus sp.	22	16	10	4	—		—	—
Trichoptera sp.	1	—	4	—	—	—	—	—
Peloscolex ferox	2	—	2	—	2	—	—	—
Ophidonais sp.	1	1	—	—	—	—	—	
Sphaerium corneum	7	2	2	—	—	1	1	
Pisidium sp.	6	5	6	2	2	—	—	
Valvata piscinalis	—	1	1	—	—	—	—	
Caenis sp.	—	—	3	—	1	—	—	
Ephemera danica	1	1	2	—	—	—	—	—
Chironomid pupae	—	—	—	—	1	—	—	—
Total numbers present	70	35	41	7	13	1	2	0
Total numbers present expressed as percentage of the total numbers present at each depth	66	34	85	15	93	7	100	0

Top layer includes layers 1 and 2. Bottom layer includes layer 3.

Table 8 shows that with increase in depth the animals become more restricted to the surface layers. One explanation of this may be that the animals which are about twice as dense at 3 m. as at 6 m. have only the same area to distribute themselves over and consequently burrow deeper into the mud, while the smaller population in the deeper regions can spread themselves more

easily over the same area. Another factor which is probably of importance is the relative amounts of available oxygen at the various depths: this is considered later in this paper.

9. Factors controlling distribution

As the time for this investigation was limited, only certain factors which were considered to have an effect on the fauna as a whole have been taken into consideration: (1) Geographical features. (2) Currents. (3) Nature of the bottom deposits. (4) Influence of plant life and the indirect influence of light. (5) Food. (6) Oxygen absorption of the mud at various depths.

Geographical features. The shape of a lake basin will have some influence on the fauna living there. Windermere is an oligotrophic lake, is trough-like, and has a sharp shelving shore-line. A lake of the eutrophic type whose shore line is gradual has usually a much higher population than the oligotrophic type. The degree of shelving will therefore influence the density of the fauna: in Windermere this point is borne out by the rapid decline in the density of the fauna between 3 and 12 m., the population at the greater depth being only 5 % of that at the shallower depth.

Effect of currents. Very little is known about the effects of currents on animals living in lakes. The currents in Windermere are not strong and seem to have little effect in the distribution of the fauna. There is, however, some evidence that currents may account for the transportation of species completely outside their usual environment. While dredging in very deep water at about 56 m. *Limnaea peregra* and *Gammarus pulex* were found on a few occasions. *Leptophlebia vespertina* occurred once at 40 m. These few examples suggest that currents may be responsible for carrying animals beyond their usual depth.

Bottom deposits. As already stated the predominant deposit is a fine mud. It was hoped to discover a correlation between the degree of fineness of the bottom deposits and the depth at which it occurs and to show that with increasing depth the degree of subdivision of the bottom particles increased. Such a correlation would furnish a reasonable explanation for the decrease in the population with increasing depth, as increasing fineness of the bottom deposits should affect the burrowing and respiratory activities of the animals present in it. That the nature of the bottom deposits does control animal distribution in the littoral zone has been shown by Moon (**6**). The fauna of a silted shore-line is in striking contrast to that of an exposed shore-line, and as previously described in this paper the effects of these differences penetrate to the 3 m. zone of the sublittoral.

In an endeavour to demonstrate such a correlation a complete analysis of the mud at various depths was undertaken. The method adopted for the analysis was that described by Hall (**2**), which consists of the sieving of the coarser particles and the observations of the rate of subsidence of the finer

particles; mud which had been dried previously and mud in the original wet condition were analysed. In the former case the dry mud was worked up with a pestle and mortar until all aggregations of particles had been broken up. By this method the proportion of the actual mineral fraction in the bottom mud was arrived at. But as, for the purposes of this survey, the actual state of aggregation of the particles of mud was of more importance than the proportion of the mineral fractions present, an analysis of the wet mud was undertaken. The mud was sieved wet and the various fractions then dried. The original dry weight of the mud sample was estimated by adding together the weight of the dried fractions. Samples of mud were taken at 4 and 12 m. from Wray Bay and Pullwyke Bay. These two depths were chosen because they represent the limits of the sublittoral zone, and any difference in the fineness of the bottom deposits should be more apparent between these depths than in the intermediate depths. The accuracy of the wet method employed was tested by comparing the results of the analysis of two samples from 12 m. from Wray Bay (Table 9). Analyses by the dry method show a much higher percentage of fine material due to the breaking up of the aggregates as they occur in the wet sample. An example of an analysis by the dry way is included for comparison. It can be seen from Table 10 that the two coarse fractions have been eliminated by this method, with a corresponding increase in the fineness of the remaining fractions. Eight complete analyses were made by the wet method, and the results demonstrate that there is little significant difference between the various particle sizes at 4 and at 12 m. (Table 11). The bottom mud of the sublittoral region is of the same uniform nature throughout, and can in no direct way be related to the zonation of the fauna.

Table 9. *Accuracy of mechanical analysis of the mud by the wet method*

12 m., Wray Bay.

Size of particles mm.		Percentage material present in the various fractions	
Maximum	Minimum	Sample (*a*)	Sample (*b*)
3·0	1·0	4·6	8·0
1·0	0·2	30·0	31·4
0·2	0·04	17·0	16·4
0·04	0·01	27·0	25·2
0·01	—	20·4	18·8

Table 10. *Grading of a mud sample by the dry method*

12 m., Wray Bay.

Size of particles (mm.)		Percentage material present in the various fractions
Maximum	Minimum	
3·0	1·0	—
1·0	0·2	—
0·2	0·04	18·5
0·04	0·01	30·0
0·01	—	48·0

Table 11

Size of particles mm.		Percentage material present in the various fractions									
		Wray Bay 4 m.			Pull-wyke Bay 4 m.	Mean %	Wray Bay 12 m.			Pull-wyke Bay 12 m.	Mean %
Max.	Min.										
3·0	1·0	2·3	9·9	9·35	9·7	7·6	6·2	8·9	4·6	4·3	6·0
1·0	0·2	21·0	26·0	28·0	28·0	27·0	24·2	24·25	31·0	20·75	25·0
0·2	0·04	24·5	16·0	16·65	20·0	19·2	24·2	18·0	17·2	23·25	20·6
0·04	0·01	24·5	20·0	22·25	21·0	21·9	23·25	27·0	26·5	23·3	25·6
0·04	—	23·0	21·0	23·25	21·0	22·0	25·25	20·0	20·75	25·0	22·0

The coarse fraction at 4 and 12 m. averages 7·6 and 6 % of the total sample. This result may not be correct, as this fraction was composed of large pieces of twigs, dead leaves, cast trichopteran larval cases, etc. The varying size and the irregular distribution of these fragments are liable to produce discrepancies in the results when dealing with only 20 gm. of material, the amount usually taken for an analysis. On this account it was decided to carry out a further determination of the percentage coarse fraction present in the bottom deposits using 500 gm. of mud. The samples were taken at 4, 6, 9 and 12 m. in Pullwyke and Wray Bay. The coarse fraction was discovered to decrease in amount gradually with increase in depth. It is hoped to prove by further experiment that there is a correlation between the decline in animal population and the falling off in the percentage of coarse material between 4 and 12 m. The variation between the percentage coarse material present at 4 m. in Wray Bay and 4 m. in Pullwyke Bay is also of interest (Table 12). This divergence indicates that at 4 m. the coarse fraction is subject to greater variations than at greater depths; this is probably due to the proximity of plant growth. Whether this variation has any connection with the comparatively scanty population in Pullwyke is a question to answer which further experiments are needed.

Table 12. *Percentage of coarse fraction in mud from various depths in the sublittoral*

	Percentage of material present in coarse fraction			
	4 m.	6 m.	9 m.	12 m.
Wray Bay	2·5	1·3	0·57	0·62
Pullwyke Bay	5·0	1·5	0·97	0·55

It was thought that the organic content of the mud might vary with the depth and that this variation might be a factor influencing the zonation of the fauna. Tests for organic content were carried out on samples of mud taken from the same localities and at the same depth as were those samples which were used for the mechanical analysis. In addition samples from the "Congo" and the profundal regions were taken. The organic content was obtained by heating the dried and weighed sample of mud for several hours at a red heat

until there was no further loss in weight. Duplicate samples were tested from each locality and depth and the mean of the two results taken. The organic content of the mud lies between 17 and 23 %. Results show that there is no significant difference in the amount of organic matter in the mud from the various regions (Table 13). The organic content of the individual fractions isolated by the mechanical analysis was next investigated. If any of these fractions showed a greater percentage of organic matter, it might be possible to explain the zonation of certain members of the fauna by supposing that they were dependent on fractions with a high organic content. Results showed that, at 4 m., fractions 3–1 mm. (the coarse fraction) had a higher organic content than the same fraction at 12 m. The other fractions agree fairly well. The significance of this result has not been investigated experimentally, but it is of interest to remember that with this decrease in the organic content of the coarse fraction with increase in depth there is correlated a decrease in the coarse fraction itself, so that the difference in actual quantity of organic matter present at 4 and 12 m. is even greater than would be thought from a consideration of Table 14.

Table 13. *Percentage of organic material in sublittoral and profundal deposits*

	3 m.	6 m.	9 m.	12 m.	16 m.	35 m.	58 m.
Wray Bay	21·0	22·0	19·0	—	—	—	—
Pullwyke Bay	19·3	18·0	19·0	18·0	—	—	—
Congo	18·0	—	20·6	19·8	—	—	—
Profundal	—	—	—	—	17·0	21·9	22·4

Table 14. *Percentage of organic material present in the various fractions*

Size of particles mm.		Wray Bay 4 m.		Pullwyke Bay 4 m.		Wray Bay 12 m.		Pullwyke Bay 12 m.	
Max.	Min.				Mean				Mean
3·0	1·0	25·0	40·0	54·0	39·6	17·0	17·0	21·0	18·3
1·0	0·2	22·3	22·7	32·0	25·6	17·0	17·0	24·0	19·3
0·2	0·04	13·0	13·7	16·0	14·2	17·0	16·0	24·0	19·0
0·04	0·01	19·7	18·0	17·0	18·2	17·0	18·0	21·5	18·8
0·01	—	19·5	18·4	13·0	16·9	16·8	19·0	21·6	19·0

In an endeavour to explain the layering of the animals in the mud, the organic content of the layers was investigated. For this purpose layers 1 and 2, described in a previous section, were grouped together to form one layer. It was found that there was no difference between the organic content of the surface and the deeper mud. The total organic material was 18–19 %. Therefore, it would appear that the distribution of the organic material in the mud is uniform to a depth of about 25 cm., which is approximately the depth of mud taken up by the grab, and cannot be in any way related to the layering of the animals.

The influence of plant life and the indirect influence of light. Light as a factor can only be treated from the indirect aspect. The seasonal variations

in the light conditions in Windermere in relation to vegetation has been investigated by Pearsall and Ullyott (**9**), who found that the penetration of light into Windermere depended chiefly on the numbers of phytoplankton organisms in the epilimnion. The greatest depth at which rooted vegetation can grow must therefore be affected by the abundance of the phytoplankton. Pearsall and Hewitt (**8**), working on the light penetration and changes in vegetation limits in Windermere, found that in a space of 12 years the maximum depth of rooted vegetation had decreased by approximately 2 m. This change was due to an increase in the numbers of phytoplankton, particularly the blue-green algae. Since the distribution of the rooted vegetation depends on the degree of light penetration, it is reasonable to suppose that even if light has no direct effect on the fauna it may be shown that animals whose mode of existence makes them dependent on plant life may be indirectly affected by changes in light intensity. Such animals have been classified as littoral migrants in this paper, because they are not common except when collections were made near the plant zone. Their distribution will undoubtedly be controlled by rooted vegetation. Forms definitely associated with this region are: Gastropods, Isopods, Leeches, Chironomid larvae and Oligochaeta. The food of leeches and Oligochaeta cannot be related to plants, but the distribution of leeches may be controlled by the distribution of the Molluscs on which they feed.

Regarding animal distribution in the deeper parts and the effect of light, nothing definite can be stated. The decrease in species between 9 and 12 m. is very noticeable. This may be due to the fact that the light at 12 m. is not strong enough to support the Algae which in shallow water grows on the surface of the mud. The majority of the animals living at this depth are detritus feeders, but they may depend to a certain extent on the Algae for food.

Food. The majority of the animals living in the mud are detritus feeders and include Ephemeroptera and Chironomidae. The nutritive value of the mud to detritus feeders may be increased by the Diatoms and other Algae growing on the surface layers. The carnivores in the sublittoral are the Tanypodinae, Cryptochironomid species, and the Sialidae. The Tanypodinae eat small Chironomids, Cladocera and also members of their own species, but they are not exclusively carnivorous as they also feed on Diatoms. *Sialis lutaria*, the only representative of the genus *Sialis*, is purely carnivorous and eats Chironomid and Tanypid larvae. Obviously the distribution of these forms will be influenced by the food available at the various depths.

In the preceding section light in relation to plants was suggested as a factor in the distribution of the sublittoral species. If the Diatoms and Algae in the mud are an important food of the fauna, then as these plants will decrease with increase in depth owing to the low light intensity, the animals dependent on them should also decrease. Again, as the detritus feeders are dependent on the organic matter present in the mud, any decrease in organic matter

should be reflected in the faunal numbers. It has been shown in this paper that the organic content of the bottom deposits is fairly uniform at all depths throughout the lake, and this would suggest that, contrary to expectations, the organic content can be of no importance in this aspect. When, however, attention is directed to the organic content of the various fractions, the decline in the coarse fraction itself seems to be significant. An explanation of this anomaly would be that detritus feeders can only make use of organic matter that is in a fairly coarse state of subdivision.

Oxygen absorption by the mud at various depths. As the estimation of the actual oxygen concentration of the mud proved extremely difficult, an attempt was made to study the rate of absorption of oxygen by the mud in the sublittoral. It was hoped that the rate of absorption would give some idea of the amount of oxygen in the mud. Samples of mud at 4 and 12 m. were taken in Wray Bay and placed in bottles with water containing a known amount of oxygen. They were treated with Winkler's reagent after an interval of 5, 10, 15, 20 and 25 min. from the time of sealing the bottles. The samples included surface mud, i.e. mud from layers 1 and 2 as described in a previous section and also mud from the bottom layer. The volume of mud used in every case was 20 c.c. Table 15 shows the amount of oxygen absorbed by 20 c.c. of mud from water containing 7·2 c.c. of oxygen per litre. The surface mud at 4 and 12 m. contains approximately the same amount of oxygen. The oxygen absorption by the deeper layer however is much greater both at 4 and 12 m., which suggests that the deeper layers contain much less oxygen and may explain why the greater percentage of the fauna distribute themselves over the surface layer.

Table 15. *Amount of oxygen absorbed by* 20 *c.c. of mud*

Time interval min.	Top 4 m. c.c.	Top 12 m. c.c.	Bottom 4 m. c.c.	Bottom 12 m. c.c.
5	5·2	4·6	6·18	6·63
10	3·6	2·9	6·15	6·85
15	3·64	1·5	5·5	6·0
20	4·0	2·75	5·4	6·64
25	2·75	2·95	5·45	6·33
Average	3·4	2·9	5·7	6·4

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Museum, Ireland, and Mr C. Oldham, who kindly identified the *Pisidia* species for me.

11. Summary

1. A qualitative estimation was made of the sublittoral and profundal fauna of Windermere.

2. The ecological importance of Windermere as a "Sergentia Lake" type is recorded.

3. A quantitative estimation was made of the sublittoral fauna. There is a gradual decrease in numbers and in species with increase in depth.

4. The numbers and species of animals at the different depths is fairly uniform throughout the sublittoral zone except at 3 m.

5. The distribution of the various groups in the sublittoral is shown graphically. The Chironomidae are the most abundant members of the fauna.

6. Possible causes of the seasonal variations in the temporary and permanent fauna are discussed.

7. The occurrence of the animals in relation to the layering of the bottom deposits is recorded. It was found that in the deeper water there was less tendency for the animals to burrow.

8. Factors which might have a controlling effect on the fauna as a whole have been investigated. They are (*a*) Physical features, (*b*) Currents, (*c*) Nature of the bottom deposits, (*d*) Organic content of the mud, (*e*) Influence of plants and the indirect influence of light, (*f*) The food of sublittoral forms, (*g*) The oxygen absorption by the mud at various depths.

REFERENCES

1. **Beauchamp, R. S. A. (1932).** "A new dredge." Int. Rev. ges. Hydrobiol. Hydrographie, 27: 467–9.
2. **Hall, A. D. (1920).** "The Soil." London.
3. **Lenz, Fr. (1925).** "Chironomiden und Seentypenlehre." Naturwissenschaften. 13: 5–10.
4. **Lenz, Fr. (1927).** "Chironomiden aus norwegischen Hochgebirgseen. Zugleich ein Beitrag zur Seetypenfrage." Nyt Mag. Natur. 67: 111–91.
5. **Lundbeck, J. (1926).** "Die Bodentierwelt norddeutscher Seen." Arch. Hydrobiol. Plankt. Suppl. Vol. 7.
6. **Moon, H. P. (1934).** "An investigation of the littoral region of Windermere." J. Anim. Ecol. 3: 8–28.
7. **Pearsall, W. H. (1921).** "The development of vegetation in the English lakes considered in the general evolution of glacial lakes and rock basins." Proc. Roy. Soc. B, 92: 259–84.
8. **Pearsall, W. H.** and **Hewitt, T. W. (1933).** "Light penetration into fresh water, II: Light penetration and changes in vegetation limits in Windermere." J. Exp. Biol. 10: 306–12.
9. **Pearsall, W. H.** and **Ullyott, P. (1934).** "Light penetration into fresh water, III: Seasonal variations in the light conditions in Windermere in relation to vegetation." J. Exp. Biol. 11: 89–93.
10. **Rawson, D. S. (1930).** "The bottom fauna of Lake Simcoe and its role in the ecology of the lake." University of Toronto Studies, No. 34, Ont. Fisheries Lab. 40: 1–183.
11. **Thienemann, A. (1915).** "Die Chironomidenfauna der Eifelmaare." Verh. Nat. Ver. Rheinl. Westf. 72: 1–58.

BREEDING RATES OF DOMESTIC RATS TRAPPED IN LAGOS, NIGERIA, AND CERTAIN OTHER COUNTRIES

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(*With 2 Figures in the Text*)

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1. Data from Lagos, West Africa

During a recent visit to West Africa I discovered that Dr J. Cauchi, Medical Officer of Health, Lagos, Nigeria, had amassed a very large body of figures relating to Black Rats (subspecies of *Rattus rattus*) and Brown Rats (*R. norvegicus*).[1] He has been good enough to forward the figures to me with the consent of the Director of Medical Services, Nigeria, and this paper reports the result of studying them.

All the rats were killed and examined in the town of Lagos. Dr Cauchi informs me that: "Many of our rats are trapped, though it is very common for owners or occupiers of property to take the rats out of the traps laid by us and throw them into the nearest gutter, public dust bin or other ground where they are picked up by sanitary labourers. A considerable number of the rats, however, perhaps a quarter or a third, are caught during anti-plague scavenging, being killed by hand, or by fumigants (capex cartridges, cyanogas dust) applied to rat-runs." The rats are taken to a central place and certain facts about species and sex are tabulated; they are also examined for the presence of plague. Dr Cauchi tells me that: "Much of the routine work has to be left to comparatively ignorant Africans, who may be taught to classify rodents into male and female and the latter into pregnant and non-pregnant." We have not, therefore, complete confidence in the result of every examina-

[1] All forms of *R. rattus* are tabulated together, quite rightly as I believe. In this paper "Black Rat" signifies *R. rattus* irrespective of colour, and "Brown Rat" signifies *R. norvegicus*. The figures from Lagos include also 1946 "shrews", a large species of *Crocidura*: they have not been studied.

tion, but the total numbers are so great and so consistent throughout the year that I feel that they have considerable value.

In the 47 consecutive months from February 1931 to December 1934 totals of 139,528 Black Rats and 7426 Brown Rats were examined. The figures for the Black Rats are well distributed over the 47 months, the highest number examined in one month (May 1931) being 4181, and the lowest (December 1934) 1647. Copies of the original figures have been deposited in the Bureau of Animal Population at Oxford, and in the libraries of the British Museum (Natural History) and the London School of Hygiene and Tropical Medicine.

Sex ratio. Among 139,528 Black Rats there were 53,556 males; that is to say, the males comprised 38·38 % of the whole (to use a different and perhaps less convenient terminology, the masculinity or number of males per 100 females was 62·29). A considerable, but rather constant, difference between the proportions of the sexes is observable for the figures for every single month. The following figures show the extreme range:

		Total rats	Males %	Masculinity
Lowest proportion of males	Feb. 1931	1990	32·8	48·8
Next to lowest proportion of males	June 1931	3959	36·2	56·5
Highest proportion of males	July 1934	1750	40·9	69·2

In view of what is shown later about the existence of a breeding season, one naturally wonders whether there is any seasonal change in sex ratio. This has been examined by working out the mean percentage of males for each of the 12 months of the year: the lowest and highest figures are 37·6 and 39·2 %, and even within these narrow limits there is no evidence of a consistent rise or fall from month to month.

Among the 7426 Brown Rats there were 3040 males: they therefore comprised 40·94 % of the total (masculinity 69·31). As the figures are relatively small it seems hardly necessary to determine the monthly percentages of males.

Breeding season. It will be remembered that the breeding season has been determined by records of pregnancies sufficiently advanced to be recognisable to the naked eye when the rat is dissected. The percentages are therefore no doubt too low, but the error is presumably consistent. In the Black Rats, the percentage of females pregnant month by month has been worked out, and the following are the monthly means based on the 47 months:

	Jan.	Feb.	Mar.	Apr.	May	June	
Total females	5481	6815	8385	7057	8344	7935	
Pregnant	759	868	980	1010	1064	1095	
%	13·8	12·7	11·7	14·3	12·8	13·8	
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Total females	6302	8123	7396	7019	7255	5860	85,972
Pregnant	979	1182	1049	1017	1037	792	11,832
%	15·5	14·6	14·2	14·5	14·3	13·5	13·76

From an inspection of the percentages, and of Fig. 1, it is at once apparent that the rats breed at all times of the year and that there are no great differences from month to month. But it will be observed that there is some indication of a difference with season, the monthly mean being always below 14 % from December to June (except April) and always above 14 % in the other five months.

The question arises whether the differences could be due to errors of sampling, or whether they are so great that they must be regarded as significant. I have tested for the significance of the differences by taking the total pregnant and not pregnant month by month, estimating the figures which would be expected if the percentage were constant throughout the year, and measuring the difference between observation and expectation by χ^2. One concludes from this test that the differences between months are so great that they cannot reasonably be attributed to "chance": P is less than 0·01: we cannot, therefore, regard the data as homogeneous.

At first sight one is inclined to assume that this proves that there is a seasonal rhythm in breeding. But this is not necessarily the case, for a seasonal increase and decrease in infant mortality, in a population in which there was no rhythm in breeding, would cause just such a phenomenon as is here observed. It is not possible, on the present figures, to say whether it is the breeding or the infant mortality which is rhythmic.

The figures for Brown Rats are not dissimilar. A total of 4386 females was examined, of which 393 were pregnant, i.e. 9·01 %. The monthly pregnancy rates are shown in Fig. 1. It will be observed that the pregnancy is consistently below 9 % in the months from December to May (reaching its lowest in April at 7·1 % in 282 females): in the months from June to November it is consistently above 9 % (reaching its highest in August with a rate of 14·6 % among 316 females).

Considering the figures for the two species together, the following points should be observed: (1) There is definite evidence that the proportion of pregnancies among females of all ages shows a seasonal rhythm. (2) The season when pregnancies (among all females) are most frequent in both species of rat runs from June to November with a peak in July or August. There is some congruence between the rainy season and this season (Fig. 1): it can hardly be supposed that this is due to any direct effect of the rain, but it seems probable that some climatic event has an effect perhaps on the quality or composition of some type of food. So far as can be observed, the gross quantity of food available in Lagos does not differ from season to season. (3) Though there is certainly a rhythm in the percentage of females of all ages which are pregnant, it is not certain that this is due to the existence of a breeding season. If the adult females were pregnant to the same extent at all seasons, a seasonal rhythm in infant mortality would produce just such figures as have been obtained.

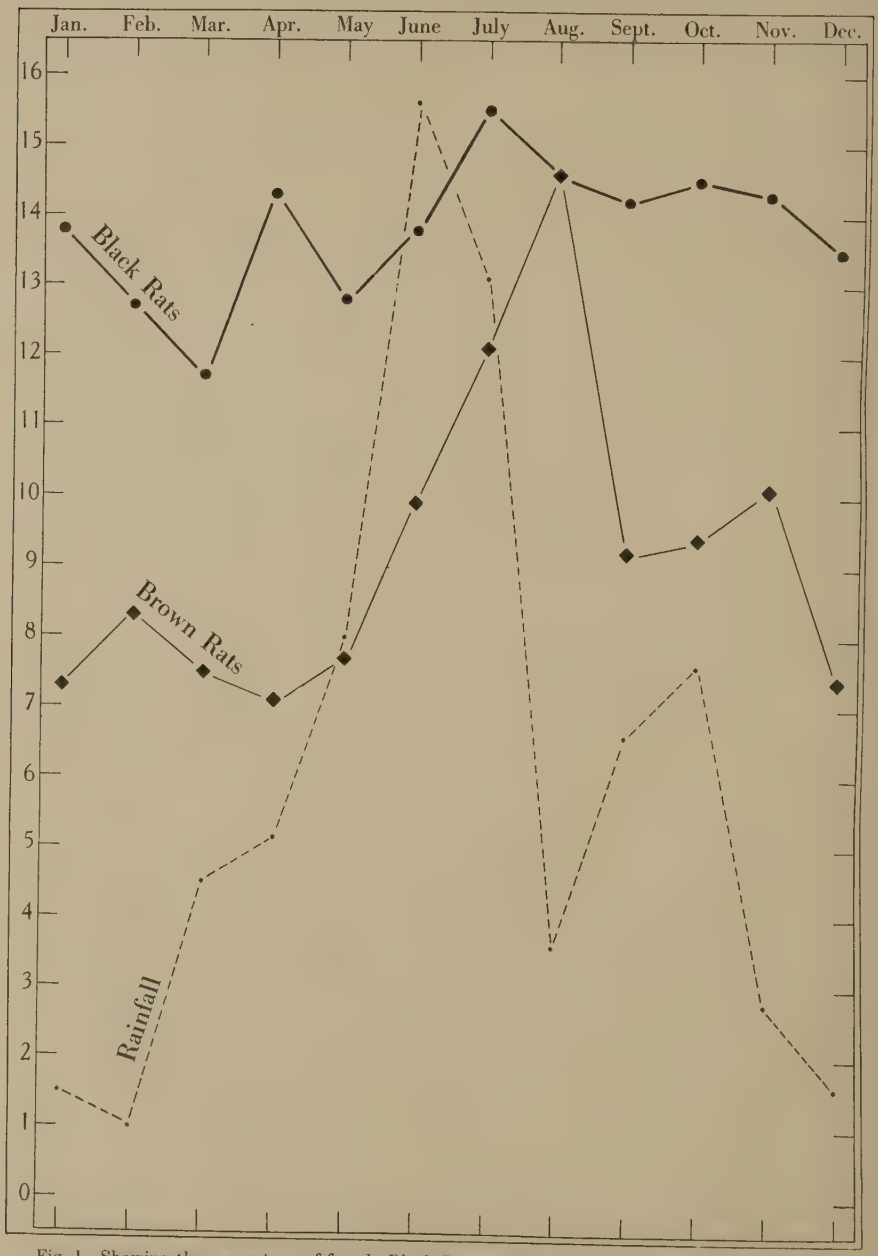

Fig. 1. Showing the percentage of female Black Rats and Brown Rats pregnant at Lagos: the figures are monthly means for the 4 years 1931–4. Also the mean monthly rainfall in inches for the same years.

2. Data from other countries

Sex ratio. Rather similar differences in the proportions of the sexes have been observed in several other countries, temperate and tropical, and in both Black and Brown Rats. I have assembled such facts as I can find in Table 1. The figures have not been collected in a precisely uniform manner, but we may assume that they are based on rats trapped and otherwise collected in connection with enquiries about plague. It is clear that the females are generally more numerous than the males in both species and nearly every place, but that the percentage of males varies greatly.

Table 1. *Showing percentage of males in domestic rats* (R. rattus *and* R. norvegicus) *as recorded by various workers*

Place	Total rats	Males %	Authors	Remarks
		Rattus rattus subspecies		
New York, U.S.A.	9,754	47·18	Williams, 1929	Trapped on ships entering port in 2 years
New York, U.S.A.	11,896	47·2	Matheson, 1931	—
Townsville, Queensland	1,157	32·15	Fielding, 1927	12 months
Kenya	3,686	44·7	Symes, 1932	17 months. Data for three towns given separately. Males 40·6–45·6 %
Dakar, Senegal	39,182	50·36	Cazanove, 1932	10 months
Java	?	28·6	Kopstein, 1931	Year
Lower Egypt	?	44–50	Bonhote, 1910	Few months
		Rattus norvegicus		
England	444	51·1	Balfour, 1922	—
Oxford, England	235	41·3	Middleton, 1929	5 months
Ipswich, England	5,997	54·6	Petrie and Macalister, 1911	Jan. and Feb. only
Newport, Wales	21,236	28·5	Matheson, 1930	5 years
Norfolk, Va., U.S.A.	1,557	43·4	Hasseltine, 1929	12 months
Townsville, Queensland	614	36·5	Fielding, 1927	12 months
Mombasa	133	39·1	Symes, 1932	—
Dakar, Senegal	5,075	46·5	Cazanove, 1932	10 months
Java	?	42·9	Kopstein, 1931	Year
Lower Egypt	?	42·0	Bonhote, 1910	Few months

In addition McCoy (1912) gives ratios collected at San Francisco, U.S.A. He says that the weekly total of rats (species not stated) always exceeded 1000, and tabulates females per 100 males (and other ratios) weekly for 3 years. The females were more numerous than the males in every week, but as no numbers are quoted it is impossible to reduce the data to a manageable form. The figures given by Jennison (1921) are not relevant to this enquiry because they were collected in Manchester at a time when female rats were being killed and males liberated. Donaldson (1924) quotes figures about the sex ratio at birth of Brown Rats bred in captivity: among 1862 young there were 46·1 % of males.

It is not by any means easy to determine the sex of a young rat, the tendency being to record females with an imperforate vagina as males. Donaldson (1924, p. 28) quoting Jackson states that "the male may be recognised by (1) The larger size of the genital papilla; (2) The greater ano-genital distance; (3) The absence of clearly marked nipples. (This test is applicable only up to the age of 16 days, i.e., before the development of hair on the ventral surface); (4) Small extent of the bare area just ventral to the anus (test applicable only after the 16th day)." He also gives a table showing weights and ano-genital distances for both sexes at certain ages from birth to an age of 42–50 days.

Breeding season. A considerable mass of rather crude facts has been collected in several countries. In nearly every place the percentages pregnant have been reckoned on the total females (of all ages); the precise interpretation of the figures is therefore open to the objection already made. It seems best to consider first the figures from Dakar, Senegal, owing to its proximity to Lagos. Cazanove (1932) has published figures obtained by trapping rats during 10 months, none being available for February and March: he tabulates his data for three races of *Rattus rattus* separately, but I have combined them here. Cazanove's figures for the Black Rat are as follows:

	Jan.	Apr.	May	June	July	
Total females	3243	1315	1360	1664	1745	
Pregnant	467	166	179	278	294	
%	14·4	12·6	13·1	16·7	16·9	
	Aug.	**Sept.**	**Oct.**	**Nov.**	**Dec.**	**Year**
Total females	1868	2064	1720	1983	2487	19,449
Pregnant	380	425	665	636	481	3,971
%	20·3	20·6	38·6	32·0	19·3	20·42

It is clear that there is a consistent rise and fall in the percentage pregnant, and that it reaches its maximum in October and minimum in April. It seems that there is no close correspondence in seasonal periodicity between Lagos and Dakar, but that is not unexpected, for though both are on the west coast of Africa there are great differences between them in climate. The same author's figures for the Brown Rats are smaller though considerable, but it seems that some error must have been made in tabulation for the percentage pregnant reaches 56·7 (171 females) in September (among all females, be it noted, not only among adults) and falls to 6·2 (532 females) in May. There is this much to be said in favour of the figures, that the rise and fall through the months is regular, and that the maxima and minima occur in approximately the same months as in the Black Rat.

From other parts of the tropics we have the following facts. In Bombay (India Plague Commission, 1907) an enormous number of rats have been examined, and the percentages are reckoned on 16,817 adult female Black Rats collected throughout the year, the percentage pregnant being 25·08.

The monthly percentage pregnant is lowest (19·3) in January, and rises steadily to a maximum in July (29·0), August (31·7) and September (30·1). The figures for Brown Rats are not very dissimilar: of a total of 27,278 adult females, 14·3 % were pregnant: the rate is lowest (9·8) in January, and actually highest (18·8) in March, the next highest months being July, August and October (all 17·0–17·8). The Bombay figures also contain information about the percentage of rats which were "young", i.e. which fell below a certain limit of weight, month by month. The information supplied about young rats is of great value because it supplements and confirms that derived from the study of pregnancies. Broadly speaking one may say that (in both species) the seasonal rise in the rate of pregnancy precedes that in the percentage of young rats. This is well seen if one groups the months into those in which breeding is more, and less, intense, and works out the mean percentage of young rats in each group of months. It is then apparent that there is some relation between the percentage of adult females which are pregnant, and the percentage of young rats in the total population in the same month: but the relation is closer if the pregnancy rate is compared with the percentage of young rats one or two months later. The figures for Black Rats are as follows:

	Six months in which pregnancy rate was under 25 %	Six months in which pregnancy rate was over 25 %
Mean per cent. young: same month	25·9	28·9
1 month later	24·6	30·2
2 months later	24·0	30·8

As the number of pairs of variables is small (12) this method of showing the relation between them appears to be preferable to a correlation coefficient, which would not be significant by conventional standards unless it were very high.

Excellent figures have also been published for Dacca in Bengal (*Report on Plague Investigation*, 1912), though the numbers are not so great. The investigators examined 2041 adult female Black Rats, of which 595 (29·15 %) were pregnant: the percentage pregnant was highest in the months February to May (maximum 43·4 % in May), and lowest in the period November to January (minimum 17·8 % in January). The percentage of young rats in all rats (5704) was 37·1 for the year as a whole, rising and falling with or a little after the pregnancy rate.

The figures published by Hirst and Vadivelu (1929) are based on a very large number of examinations of *R. rattus kandianus*, made in Colombo, Ceylon, in 1914. The percentage of all females pregnant is at its lowest (5·86 %) in March, and rises to two peaks, one in April to July, the second in October and November; the highest percentage (15·85) is for November. No figures are given for January and February, and no actual number per month, though the total females was 11,096. The authors conclude that "it would appear

that reproduction is most active during the rainy seasons, at the onset of the south-west and north-east monsoons".

Petrie and Todd (1923) have published figures based on nearly 40,000 Black Rats examined in Upper Egypt during 24 consecutive months. They give the percentage of adult females pregnant (9788 examined), month by month in Asyut: the figure is at its lowest (18–20 %) in the months from November to January, and at its highest (40 % and over) in the hotter months of the year. These very valuable figures are supported by facts on the proportion of young rats (65 gm. and under, 8012 examined) to all rats (26,281 examined). The percentage of young rats in the total rat population is 17-21 % from December to March, and rises to a maximum of 40–43 % in July or August (one April showing the exceptional figure of 55 % in 536 rats). It will be seen that the figures for pregnant and for young rats support one another, the maxima and minima in the percentage of young rats falling a little later in the year than those for pregnancy, as would be expected.

Figures from three places in Kenya, Nairobi, Kisii and Mombasa have been published by Symes (1932): the rats were collected over a period of 17 months. The numbers are not very large, and there are certain inconsistencies in them; compare for instance:

Jan. 1929	Nairobi	Black Rats	54 females	65 % pregnant
Jan. 1930	„	„	250 „	27 % „

In commenting on his figures Symes draws the conclusion that in Nairobi there is one season of increased breeding in the early months of the year, and a second in September or October. He proceeds to make the following interesting remarks: "This rat, inhabiting as it does the dwellings and stores of man, is to a very great extent independent of purely natural stimuli to breeding and may vary suddenly and unexpectedly as the result of some quite artificial factor such as an increase of grain storage. It is probable too that small communities of this species may exhibit variable degrees of increase during any one period, as the result of very localised conditions. Thus rats inhabiting a bazaar and certain commercial areas where human goods are stored may increase enormously whilst their relatives infesting residential areas in another part of the town may show no similar rise in numbers. Similarly during a 'famine' year *R. rattus* in native reserve areas may experience some great difficulty in obtaining a bare subsistence, whereas their luckier brethren on a large estate controlled by Europeans might well be living in comparative luxury; the breeding rate and season of communities living under such different conditions would most certainly differ very considerably. For this reason, therefore, it seems inadvisable to suggest that the breeding season for any one species of rat is necessarily the same in all districts except in the very broadest sense; local conditions must obviously play an important part in hastening or postponing, intensifying or checking reproduction."

Some interesting figures from the Hawaiian islands have been published by Eskey (1934). He dealt with large numbers of Black Rats of several races, collected in several parts of the archipelago, and separated adult from young females: pregnancy was most common (25 % of adult females) in August, and least (under 4 %) in November, December and January.

We may now pass to facts collected outside the tropics. Cleland (1918) has published data collected during 3 years at Perth, Australia. The animals were "almost entirely" *R. rattus*. The percentage of females pregnant seems to vary rather erratically, and figures are not given for every month; but the rates are high (over 20 %) for the summer months, from October to February, and fall to 9 or 10 % in April and May.

Figures are also available from the east and the west side of the United States. On the east coast, Hasseltine (1929) worked for 12 months at Norfolk, Virginia; practically all the rats were *R. norvegicus*. There were 881 females of this species, of which he classified 620 as adult: the pregnancy rate in the adults was 34·8 % for the year. As there were always less than 100 females in any one month, the monthly pregnancy rates are not very reliable: but it is clear that breeding occurs all the year round, and that the percentage of females pregnant is lowest in January and highest in the period from March to June.

From the west side of North America one may quote the figures published by McCoy (1912). In San Francisco, California, he found that rats (presumably Brown Rats) bred at all seasons, but that the percentage pregnant was higher in summer than in winter: his percentages are unusually low, 4·5 % in winter, 5·6 % in summer. Williams (1929) has published a large collection of facts, carefully tabulated, about rats caught in the Port of New York; but as all his rats came from ships arriving from every quarter of the globe, the figures are not of value in the present enquiry.

At this point it is perhaps relevant to remark that many authors have published figures about the number of embryos found. In several places there is no evidence that there is any seasonal difference in the mean number of embryos per pregnant female for either species of rat. The figures of Hasseltine (1929) for Norfolk, Virginia, McCoy (1912) for San Francisco, and Hirst and Vadivelu (1929) for Colombo, Ceylon, are the most complete in this respect. On the other hand, according to Petrie and Todd (1923), who examined 2226 pregnant female Black Rats at Asyut in Upper Egypt over a period of 24 months, the mean number of embryos was 5·8, and there was a small but regular variation in the number, the maximum occurring at the season when the percentage of pregnancy was highest. It is unfortunate that no figures are given, except the mean for the whole period.

One may perhaps summarise these facts about breeding seasons by calling attention to the following points: (1) Even in the equable climate of Lagos (p. 54) there is definite evidence that the proportion of pregnancies (among

females of all ages) shows a seasonal rhythm. It is not, therefore, surprising to find similar evidence in every country from which figures are available. (2) The season when pregnancy is commonest in Brown and Black Rats coincides approximately not only in Lagos (p. 55) but in the other places in which both species occur in sufficient numbers, for instance Bombay and Dakar (the figures for Brown Rats from Dakar being open to criticism). (3) Generally speaking the breeding season appears to coincide with the warm season in temperate and subtemperate climates. But it appears that in places which have a monsoon (Lagos, Bombay, Dakar) the relation between climate and breeding is not so simple. It seems probable, as Symes (1932) suggests, that breeding is largely a matter of nutrition; that may well depend on harvests, and indirectly on climatic events.

3. Discussion and suggestions

The purpose of this paper is to suggest ways in which valuable information might be obtained about the biology, and in particular the reproductive powers, of domestic rodents. It seems that with rather more attention to principles the medical officer of a port, or the pathologist in charge of a laboratory, might considerably increase our knowledge of the biology of rats without greatly adding to the time spent in collecting the data: indeed, the labour might frequently be reduced, and more information gained from smaller collections of rats. It is no part of my purpose to outline a scheme of research such as might be undertaken by an expert in the physiology of sex.

It is clear that there are considerable inconsistencies in figures published from different places, but one cannot say whether these are due to actual differences in the rats, or to different and imperfect methods of collecting. The most probable source of error in the figures is in the *sampling*. The great majority of the rats have been trapped, but it is not certain that this gives a representative sample: indeed it seems highly probable that young rats are more easy to trap than old ones, and trapping may also be selective in respect of sex. It is highly desirable that investigators should collect and publish data from rats killed in some unselective way: for instance, one would welcome figures collected when the whole community of rats in a warehouse or ship is gassed. Until the sampling technique has been more critically examined we cannot place much reliance on the existing sex ratios, or figures about pregnancy or the abundance of young rats.

But it seems that existing records may also be imperfect owing to errors made in examining the rats and tabulating the results. Attention should be given to the following points:

In considering *sex ratios* particular care is needed in determining the sex of young rats (p. 58). It would also be valuable to record the sexes of very young rats in the nest, or of large unborn embryos.

In determining the *breeding season* or the season at which breeding is most intense the majority of the authors state the number of pregnancies observed among all the female rats examined. But it is clear that in figures given so crudely a seasonal rhythm in breeding may be masked. Suppose, for instance, that increased breeding begins in June, the proportion of young rats may be high in July and August. These young rats, none of which are breeding, dilute the population and reduce the percentage pregnant. Seasonal changes in infant mortality (due to starvation, floods, diseases) would also produce seasonal changes in the proportion of all females pregnant, even if the proportion of adults pregnant were constant. These errors could be avoided if authors would standardise their pregnancy rates by basing them on adult females, but to do this some accepted criterion of maturity is required.

It is clear that a full study of ovaries, etc., will not generally be possible, and that the standard must be simple of application, and it appears that an arbitrary limit of weight will best meet the needs of the case. For most purposes one might accept the Indian Plague Commission's standard, that any *R. rattus* is immature if it weighs under 70 gm., and that the limit for *R. norvegicus* is 100 gm. The standard adopted by Petrie and Todd (1923) in Upper Egypt was that any Black Rat weighing 65 gm. or less was immature. It should not, however, be forgotten that pregnancy has been recorded in an Indian *R. rattus* weighing only 50 gm. (Lloyd, 1909); this, however, was the lowest weight among about 2000 pregnant rats. Hirst and Vadivelu (1929) weighed 50 pregnant *R. rattus kandianus* at Colombo, Ceylon; the range was 87–187 gm., the mean 127·72 gm. A collection of data serving to delimit the lowest weight at which pregnancy occurs would be of considerable value. It is quite possible that the limit depends on nutrition, and is different in different places. In tabulating large masses of data it would probably be best to place the weight limit rather high, for one wishes to work out pregnancy rates, etc., on an all-adult population.

Balfour (1922) used the presence of the corpus luteum as a sign of maturity: he recorded its absence in one Black Rat of 188 gm. and several Brown Rats up to 170 gm. Prof. Brambell points out that the criterion is dangerous in the hands of the inexpert, for animals in anoestrus or in late lactation anoestrus might be recorded as immature.

Apart from those quoted, the only authors who distinguished adult females are Eskey and Hasseltine, who do not specify the criteria upon which they relied.

Most authors have been content to publish a mean *number of embryos* per pregnant female. It is evident that some measure of the scatter about that mean is desirable: for rough purposes a maximum and minimum may be sufficient, but it is generally advisable to publish a frequency distribution, or a standard deviation. It is preferable to give the number of embryos per pregnant female, rather than average the embryos among all females whether pregnant or not, as was done by Symes (1932).

It seems that it would be valuable, and easy, to record information about *lactation*, ability to press milk either from the nipple or from an incision in the gland being regarded as the only criterion.

The work of *tabulating* is greatly facilitated if each rat is booked separately on a card: an appropriate card is shown (front and back) in Fig. 2. The size may be about $3\frac{1}{2}$ by 6 in. The paper by Webster (1932) gives valuable notes about recording fleas and lesions due to plague. The particulars are, of course, subject to alteration to suit local conditions. If the information is carded it is extremely easy to discover (as an example) how many female Black Rats weighing 80–90 gm. have been examined and whether any were pregnant:

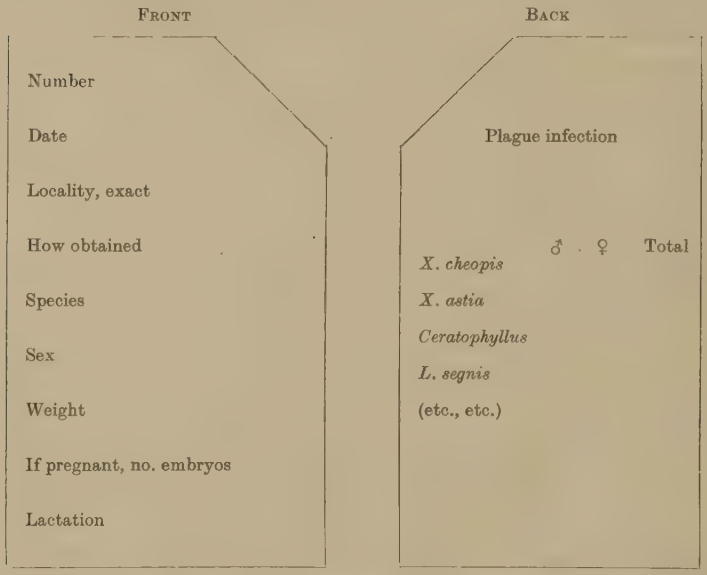

Fig. 2. Type of card appropriate for booking data derived from the examination of one rat.

it would be a matter of some labour to extract this from a book. It is very much to be desired that investigators should standardise their methods of recording, and of tabulating, so as to produce comparable results.

In *publishing* it is important to give actual numbers and not percentages alone, or at least one must give enough actual numbers to enable the rest to be calculated if required. The need is evident if one considers the large body of work assembled and published by McCoy (1912). For every week for a period of 2 years he publishes the number of female rats per 100 males, and the percentage of the females which were pregnant. But he gives no actual numbers, so that one cannot convert the weekly figures to monthly figures, or compare a particular week in one year with the same week in the next.

4. Acknowledgments

It is a pleasure to acknowledge the help which I have received in compiling this paper. The published information is very scattered and some of it has perhaps escaped me, but Mr C. Elton and Capt. R. L. Sheppard, Secretary of the Bureau of Hygiene, have done what they could to make the collection of references complete. The paper has been read in draft by my colleague, Major P. G. Edge, by Mr Elton and by Prof. F. W. R. Brambell, all of whom have made valuable suggestions.

5. Summary

The author has collected published and manuscript information from many parts of the world relating to Black and Brown Rats: particular attention is given to sex ratios and to the seasons when breeding is more or less intense. Much of the existing information, though collected with great labour, is of little scientific value because sufficient thought was not given to general principles at the time of collection. It is for this reason that no general conclusions can be drawn.

A number of suggestions are made as to the way in which figures should be collected and tabulated. It is felt that if these are followed it would not be difficult to get accurate knowledge about the potential and actual increase of populations of rats. This could be done without greatly adding to the labour which is at present spent in health departments in many parts of the world.

References

Balfour, A. (1922). "Observations on wild rats in England, with an account of their ecto- and endoparasites." Parasitology, 14: 282–98.

Bonhote, J. L. (1910). "On the varieties of *Mus rattus* in Egypt; with general notes on the species, having reference to variation and heredity." Proc. Zool. Soc. Lond. pp. 651–65.

Cazanove (1932). "Le problème du rat dans le territoire de Dakar et Dépendances." 2e Conf. Internat. du Rat, Paris, Oct. 1931: 95–146.

Cleland, J. B. (1918). Presidential Address by the President, Roy. Soc. of New South Wales, Sydney, May 1, 1918. Issued Sept. 5, 1918.

Donaldson, H. H., editor (1924). "The rat: reference tables and data for the albino rat (*Mus norvegicus albinus*) and the Norway Rat (*Mus norvegicus*)." 2nd ed. Mem. Wistar Inst. Philadelphia.

Eskey, C. R. (1934). "Epidemiological study of plague in the Hawaiian Islands." U.S. Publ. Health Service, Bull. No. 213.

Fielding, J. W. (1927). "Observations on rodents and their parasites." Roy. Soc. N.S. Wales, 61: 115–34.

Hasseltine, H. E. (1929). "Rat-flea survey of the Port of Norfolk, Va." Publ. Health Rep., Washington, 44: 579–89.

Hirst, L. F. and **Vadivelu, K. (1929).** "The rat-flea survey of Kandy." Ceylon, Sessional Paper, No. 13.

India Plague Commission (1907). "The epidemiological observations made by the Commission in Bombay City." J. Hyg. 7: 724–98.

Jennison, G. (1921). "Rat repression by sexual selection." J. Roy. Sanit. Inst. 41: 358–63.

Kopstein, F. (1931). "Die Ökologie der javanischen Ratten und ihre Bedeutung für die Epidemiologie der Pest." Z. Morph. Ökol. Tiere, 22: 774–807.

Lloyd, R. E. (1909). "The relation between fertility and normality in rats." Rec. Indian Mus. 3: 261–5.

Matheson, C. (**1930**). "Some notes on the brown and the black rat in the City and Port of Cardiff." Trans. Cardiff Nat. Soc. 61: 55–65.

Matheson, C. (**1931**). "The brown and the black rat in Wales." Rep. Nat. Mus. Wales.

McCoy, G. W. (**1912**). "Notes on the bionomics of rats and ground squirrels." Publ. Health Rep. Washington, 27: 1068–72.

Middleton, A. D. (**1929**). "*Leptospira icterohaemorrhagiae* in Oxford rats." J. Hyg. 29: 219–26.

Petrie, G. F. and **Macalister, G. H.** (**1911**). "Report upon the examination of rats collected in Suffolk and Essex, for plague infection, Jan. 16 to Feb. 14, 1911." Rep. Local Govt. Board, Publ. Health, New Series, No. 52: 56–62.

Petrie, G. F. and **Todd, R. E.** (**1923**). "A report on plague investigations in Egypt." Rep. Publ. Health Lab., Cairo. Plague Report.

Report on Plague Investigations in India (**1912**). "Observations on plague in Eastern Bengal and Assam." J. Hyg. Plague Suppt. 1: 157–92.

Symes, C. B. (**1932**). "Notes on rats, fleas and plague in Kenya (II)." Rep. Med. Res. Lab. Kenya, No. 3.

Webster, W. J. (**1932**). "Notes on the study of plague in the field." Indian Med. Gaz. 67: 693–6.

Williams, C. L. (**1929**). "A rat and a rat-flea survey of ships at the port of New York." Publ. Health Rep., Washington, 44: 443–76.

THE INFLUENCE OF ECOLOGICAL FACTORS ON THE MEDITERRANEAN FLOUR MOTH, *EPHESTIA KÜHNIELLA* AND ITS PARASITE, *NEMERITIS CANESCENS*

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(*With 4 Figures in the Text*)

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1. Introduction

The interactions of insect hosts and their parasites under natural environmental conditions have been studied by a number of investigators, in some cases very thoroughly. The ecological factors in nature are, however, so variable and complex that they cannot be measured or expressed even with approximate accuracy. Such studies, while helping the investigator in making general and broad predictions, cannot yield definite knowledge, unless they are corroborated by experimental evidence under controlled environmental conditions.

A number of studies made under accurately controlled temperatures are available, but very little work has so far been done under conditions of properly controlled humidity. Webster and Phillips (1912) determined the threshold of development of the host, *Taxoptera graminum* Rond., and its parasite *Aphidius testacyepes* Cress., and found that the development of the parasite ceased at a temperature higher than that of the host, indicating thereby that low temperature was more favourable to the host than to the parasite.

Hefley (1928) in his studies on the Hawk moth, *Protoparce quinquemaculatus* Haw., and its parasite *Winthemia quadripustulata* Fab., accurately controlled both temperature and humidity. He found that at 27° C. viability of the host was greatest with 0 % relative humidity, that of the parasite with 73 % relative humidity.

Payne (1933) studied the fecundity and development of *Ephestia kühniella* Zeller and its parasite *Microbracon hebetor* Say. at constant temperatures but without any regard to humidity. She found that the slow strain of the host could complete the developmental cycle between 8° and 34° C., the fast strain between 10° and 32° C. The parasite could develop and breed between 14·5° and 34° C. At temperatures above 20° C. the parasite was able to overtake the host, since it could complete two generations with one of the host larvae. Below 15° C. the parasite could not complete its development, and so there was no possibility of its controlling the host. Above 32° C. the parasite had a definite advantage over the host: thus, high temperature was favourable for the parasite, low temperature for the host.

The Mediterranean flour moth, *Ephestia kühniella* Zeller, is a well-known serious pest of farinaceous meals. It is parasitised by *Nemeritis canescens* Gravenhorst (Ichneumonidae), the importance of which has not been recognised till recently. Very little is known about the life history and habits of this parasite, much less about the influence of controlled environmental conditions upon its development.

2. MATERIAL AND METHODS

Source of material. In December 1933, a stock of *Ephestia kühniella* larvae and about a dozen *Nemeritis canescens* adults were obtained from the Biological Field Station, Slough. Cultures were started at the Entomological Field Station, Cambridge, so as to ensure a constant supply of material.

Breeding of host. General breeding was carried out in a room heated to 22–24° C. The humidity of the air was not controlled, but the hygrograph records showed a relative humidity (R.H.) of 65–75 % during most of the time. The breeding technique described by Mansbridge (1933) was adopted with some modifications. The moths were collected daily from breeding jars with a sucking tube and liberated for oviposition into a dish. The bottom of the dish was lined with black paper, as this greatly facilitated counting, and the eggs were easily brushed off the paper without injury.

Since unfertilised eggs are not uncommonly laid by *Ephestia*, therefore, in order to avoid blank cultures, it was found convenient to start with freshly hatched larvae instead of eggs. 200–300 freshly hatched larvae were liberated on Quaker oats, in square confectionery jars measuring 4 × 4 in. and 7 in. high. The jars were covered with cotton gauze stretched and glued on heavy metal rings, about 2 in. wider than the mouth of the jar. The weight of the ring kept the gauze tightly pressed to the top of the jar. Rolls of corrugated paper placed inside the jars offered a suitable place for pupation. By starting a fresh culture every other day an abundant supply of different stages was always available.

Precautions. The Quaker oats provided for food were always sterilised for about an hour at 60–70° C. in order to eliminate the introduction into cultures of fungi, mites, etc. In spite of this, at high humidity and high temperature fungi sometimes appeared in experimental dishes. The only source were the *Ephestia* larvae themselves, and in later experiments this trouble was avoided by sterilising the eggs for 5 min. in 90 % alcohol and then washing them with distilled water.

It is not desirable to breed parasite and host near together, as the stray parasites are likely to infest new host cultures and render a supply of parasite-free host larvae extremely doubtful. Parasite cultures were therefore kept in the Zoological Laboratory, about 1 mile from the Entomological Field Station.

Breeding of parasite. For parasite breeding experiments, a known number of full-grown host larvae were liberated with food in glass dishes, 5 in. in diameter and 2·5 in. high. Since all the parasites are females and breed parthenogenetically, it was only necessary to liberate a freshly emerged parasite among the hosts and to cover the dish with cotton gauze.

Adult parasites live longer when fed on honey or sugar solution. So a piece of cotton lint soaked in a solution of 1 part honey and 3 parts water was provided. As parasites cannot feed on thick honey it was necessary to pour

a few drops of fresh honey solution on the cotton lint every other day. This method was later modified by using a wick of cotton lint dipped in a solution of honey in a small tube. Thus a constant supply of honey solution was ensured. At high temperatures, however, the solution fermented very soon and frequent renewal was necessary.

Times of observation. Observations were ordinarily taken once a day at 9 a.m. except where the short duration of a stage warranted more frequent attention.

Apparatus for the control of temperature. For controlling high temperatures of 33°, 30°, 27° and 23°C. electric incubators were employed. For low temperatures of 18°, 15°, 12°, 5° and 0°C. the use of constant-temperature rooms was granted by the courtesy of the Superintendent, Low Temperature Research Station. The temperature of these rooms was controlled with a variation of not more than $\pm 0{\cdot}1$°C., that of the high-temperature incubators not more than $\pm 0{\cdot}2$°C. Owing to their small size the temperature in different parts of the incubators remained equable, even without any arrangement for circulating the air. These incubators were surrounded by a double-walled water jacket, which with its large thermal capacity ensured minimum fluctuation of temperature.

Relative humidity and saturation deficiency. With regard to the influence of moisture on living organisms, Buxton (1931) suggested that saturation deficiency (S.D.) may prove a better measure of the rate of evaporating power of air than R.H. He has shown that when Fawcett's data about the prevalence of *Xenopsylla cheopis* is converted from R.H. to S.D., the latter was always under 8·5 mm. of mercury. This agrees with Brook's generalisation that epidemics of plague may start and increase over a wide range of temperature provided the S.D. is 8·5 mm. or less. Again, there is considerable experimental evidence to show that optimal requirements of insects in terms of percentage R.H. rise with the rise in temperature (Parker, 1930; Menusan, 1934). Kirkpatrick's conclusions (1923) on the resistance of insects to high temperatures by high R.H. are compatible with the idea of S.D.

Notwithstanding this and other similar data, many investigators have employed for comparison similar values of R.H. at different temperatures. Some have followed this method merely because of convenience, e.g. Lund (1934) who, in his work on *Trichogramma minutum*, admits this frankly. Others, notably Lathrop, Janisch and Uvarov, maintain that the rate of evaporation as registered by an evaporimeter is not a satisfactory index of insect metabolism. While it is quite true that the rate of evaporation from an insect's body is not a mere physical process, it is claimed that S.D. of air is a better approximation to the absolute measure of the evaporating power of air than R.H. For this reason in the present work similar values of S.D., viz. 0, 3, 9, 14, 21 and 32 mm., have been employed at different temperatures.

Control of relative humidity. Humidity was controlled mainly by using

saturated solutions of different salts. The percentages of R.H. obtained with different chemicals are shown in Table 1. These figures agree fairly well with the values reported by Janisch (1933). In some cases where the desired value of R.H. could not be obtained by means of salts, sulphuric acid solutions were employed. These were used only where absolutely necessary because, while dealing with feeding stages of insects, particles of food are likely to fall into the solution, liberating SO_2 which not only disturbs the humidity-regulating power of the solution but is also injurious to the insects. Moreover, for very high and low humidities the concentration of sulphuric acid solutions changes too quickly. KOH solutions were not employed because the accumulative absorption of CO_2 given out by larvae would have greatly disturbed the humidity-regulating power of the solutions by the conversion of hydroxide into carbonate. KOH, however, seems to be suitable where the insects are few and experiment is short.

Table 1. *The relative humidities obtained by using different chemicals*

Temp. °C.	Required S.D. mm.	Chemical used	Approximate % of chemical in the solution	% R.H. obtained
0	3	$CaCl_2$	Saturated solution	35
5	3	H_2SO_4	42	53
12	3	H_2SO_4	33	70
	9	$ZnCl_2$	Saturated solution	10
15	3	NaCl	,,	76
	9	H_2SO_4	55	27
18	3	NH_4Cl	Saturated solution	80
	9	K_2CO_3	,,	43
	14	$ZnCl_2$	,,	11
23	3	KCl	,,	86
	9	$Ca(NO_3)_2$	,,	56
	14	$CaCl_2$	,,	32
	21	P_2O_5	Pure	0
27	3	H_2SO_4	21	88
	9	H_2SO_4	36	66
	14	K_2CO_3	Saturated solution	45
	21	H_2SO_4	60	19
30	3	KNO_3	Saturated solution	90
	9	$NaNO_3$	,,	71
	14	H_2SO_4	42	54
	21	$CaCl_2$	Saturated solution	32
	32	P_2O_5	Pure	0
33	3	KnO_3	Saturated solution	91
	9	NaCl	,,	76
	14	H_2SO_4	38	62
	21	$Ca(NO_3)_2$	Saturated solution	44
	32	H_2SO_4	62	15

Desiccators of a specially large size, 10 in. high, with top diameter 12·5 in. and bottom diameter 9·5 in., were used, but the distance between the solution and the top of breeding dishes was not more than 3 in.

Recording of relative humidity. It is commonly taken for granted that the desired R.H. is maintained, once the corresponding solution of the chemical has been placed in a desiccator. This is not so. The recording of R.H. is as important as the recording of temperature. To maintain low humidities water is being constantly absorbed by salt solutions, while to keep a high percentage of R.H. water is being given out, so that the addition of salt in the former case and that of water in the latter case is essential. That being so, it is necessary to test the humidity from time to time. Unfortunately no very rapid and at the same time convenient way of measuring humidity in small spaces is yet available. Hair hygrometers are themselves susceptible to permanent changes under the influence of variation of temperature and of humidity. For this reason it was found necessary to standardise the hygrometers with a whirling wet- and dry-bulb psychrometer once a week. It may be mentioned, that, even so there is a possible error of ± 3 % in R.H.

3. The development and fecundity of *Ephestia kühniella* at constant temperatures and saturation deficiencies

(*a*) *General*

The biology of *Ephestia kühniella* has been studied under natural conditions by Burkhardt (1919), Hase (1924), Candura (1928), Voukassovitch (1929) and others. Brindley (1930) was the first to study its development under controlled conditions, at 30° C. and 73 % R.H. Von Gierke (1932) worked out the number of larval moults at constant temperatures of 18° and 25° C.; Norris (1933) the factors affecting fecundity, with particular reference to biological causes; and Payne (1933) the rates of development at several constant temperatures. Opinions have also been expressed with regard to the probable influence of the R.H. of the air, but there are no experimental data in support of these. In order to elucidate this point particularly, experiments on the breeding of *Ephestia kühniella* were carried out at three constant temperatures (18, 23 and 30° C.) and S.D. of 3, 9, 14 and 21 mm.

(*b*) *Number of eggs*

Widely different figures for the number of eggs laid per female have been given. Jakobi (1905) considers 60 eggs per female as an average. Landois (1885) quoted by Norris (1933) places the number at 678, but based his figure on the number of egg rudiments counted in the ovaries of a single female: the majority of workers tend to give smaller figures. Summing up the previous data, Norris (1933) remarks: "This disparity may be accounted for, in part by difference in the food materials used or by the existence of distinct strains differing in the number of eggs produced. It is, however, highly likely that it is largely due to inclusion in record of other workers of abnormal individuals which lay only a small proportion of eggs." In *Ephestia kühniella*, sterile or partially sterile individuals having low fecundity and laying infertile eggs frequently occur.

The total numbers of eggs laid by a known number of pairs of moths bred under controlled conditions of temperature and S.D. are given in Table 2. The average number of eggs laid per female is highest at 23°C. It is adversely affected by rise in the S.D. of the air. A large proportion of the eggs laid at high temperature (30°C.) was infertile. Shortly after oviposition the fertile eggs can be distinguished from the infertile eggs by their turgidity, the developing embryo, and the coloured egg yolk visible through the egg shell. The infertile eggs, on the other hand, shrivel up quickly in a characteristic manner and appear translucent or even transparent. Counts of infertile eggs based on a random sample of 500 eggs in each case are given in the last column of Table 2. There is considerable sterility at high temperature and high S.D. Brindley also observed a marked degree of sterility at 30°C. and 73 % R.H. Norris laid so great a stress on the incidence of unsuccessful pairing and the resulting sterility to temperature that she almost ignored the influence of humidity of the air. She states: "At temperatures as low as 27°C., it is just possible that humidity may play an auxiliary part (in bringing about sterility) but at 30°C., humidity is of no importance." Payne, on the other hand, seems to have overlooked this increased sterility at high temperature. In calculating the reproductive potential she has used the maximum fertility factor of 70 % at all the temperatures above 20°C.

Table 2. *The number of eggs laid by moths under different conditions*

Temp. °C.	S.D. mm.	No. of pairs	Total no. of eggs laid	No. of eggs per female	% fertility*	No. of fertile eggs per female
18	3	23	4505	196	86	169
	9	21	3948	188	79	149
	14	12	1702	142	68	97
23	3	20	4241	212	86	182
	9	20	4304	215	82	176
	14	15	3074	205	78	160
	21	11	1883	171	66	113
30	3	28	5710	204	40	82
	9	19	3134	165	27	45
	14	12	1322	110	22	24

* The percentage fertility is based on 500 eggs taken at random in each case.

The figures regarding the average number of eggs laid per female given in Table 2 are low, owing to the occurrence of sterile individuals in each lot. The number of eggs laid by successfully paired females alone is shown in Table 3. The fecundity of such females rises with the temperature, but falls as the S.D. increases. Thus, high temperature, while it increases the fecundity of *Ephestia kühniella*, markedly reduces its fertility. Among the causes of low fertility, unsuccessful pairing is by far the most important factor (Norris, 1933).

The longevity of copulated females is shown in the last column of Table 3. The duration of adult life is shortest at high temperature (30°C.) and high S.D. (14–21 mm.).

Table 3. *The longevity of, and the number of eggs laid by, normally copulated females.* (*Averages of five pairs*)

Temp. °C.	S.D. mm.	No. of eggs per female	Life of female days
18	3	305	10·4
	9	296	10·0
	14	206	9·0
23	3	331	8·0
	9	337	8·1
	14	299	6·8
	21	225	6·4
30	3	355	6·5
	9	342	6·1
	14	201	5·5

(*c*) *Rate of development*

1. *Existence of two strains.*

Ephestia kühniella possesses a number of strains developing at different rates, even under similar environmental conditions. Two of these, a fast and a slow strain, predominate. This fact was noticed by several workers but was not given the attention it deserves until Payne (1933) gave experimental evidence in support of this. Chittenden (1896) recorded the presence of some larvae with "protracted" development. Burkhardt (1919) observed the same differences in the rate of development. He noticed that, from a batch of larvae hatched on the same day, some acquired wings while others were still in the larval stage. Hase (1927), while studying the development of eggs at constant temperatures, noticed two peaks for the incubation period, the larvae of which he called "Frühschlüpfer" and "Spätschlüpfer". His failure to recognise them as two distinct strains led him, like many other workers, to express the incubation period by the average of the two peaks, thus obliterating any true picture of either of the two strains. The experiments recorded in this paper confirm Payne's observations and establish beyond doubt the existence of two strains developing at widely different rates.

2. *Influence of temperature.*

It will serve no useful purpose to summarise previous data on the rate of development in different seasons under conditions of uncontrolled temperatures. Payne has given the duration of the egg, larval and pupal stages of the two strains at different constant temperatures. From the similarity of the graphs obtained by plotting the duration of development of the two strains against temperature, she found that although the durations of the life cycle of slow and fast strains differ markedly, yet the effect of temperature on the rate of development of two strains is approximately the same. Tables 4 and 5 give the duration of the egg stage, and the duration of larval and pupal stages respectively. The results obtained agree with those of Payne fairly well. The variations that exist are explained by the fact that her breeding material was

exposed to unknown and possibly varying humidity of air which has considerable influence on the rate of development. With 3 mm. S.D. the average duration of the egg stage of the two strains is 3·6 and 5 days at 30°C., and 9·3 and 11·2 days at 18°C. The duration of larval stage is 26·3 and 32·4 days at 30°C. and 59·9 and 72·8 days at 18°C., and the duration of the pupal stage is 6·1 and 8·4 days at 30°C. and 12·9 and 21·0 days at 18°C.

Table 4. *The incubation period of eggs under different conditions*

Temp. °C.	S.D. mm.	No. of viable eggs	Fast strain days	Slow strain days
18	3	1031	9·3	11·2
	9	1146	9·5	11·5
	14	824	10·0	12·5
23	3	1837	5·5	6·5
	9	1424	5·8	6·8
	14	1193	6·0	7·0
	21	1161	6·0	7·0
30	3	843	3·6	4·0
	9	1047	3·7	4·5
	14	751	3·75	4·7
	21	1360	3·8	5·0
	32	1034	3·8	5·0

Table 5. *The larval and pupal periods under different conditions*

Temp. °C.	S.D. mm.	Larval period: No. of larvae	Larval period: No. of days	Larval period: Standard error	Larval and pupal period: No. of pupae	Larval and pupal period: No. of days	Larval and pupal period: Standard error	Pupal period days
				Fast strain				
18	3	351	59·90	0·18	324	72·80	0·18	12·90
	9	212	66·07	0·26	197	85·27	0·27	19·20
	14	63	75·52	0·57	50	99·58	0·73	24·06
23	3	373	42·42	0·19	352	51·82	0·17	9·40
	9	408	57·11	0·18	371	69·68	0·19	12·57
	14	262	65·44	0·18	193	80·63	0·24	15·19
	21	67	75·21	0·68	41	91·68	0·60	16·47
30	3	283	26·30	0·17	246	32·37	0·19	6·07
	9	220	29·48	0·20	174	35·53	0·21	6·05
	14	85	32·67	0·35	71	39·51	0·38	6·84
	21	26	59·62	0·89	17	67·00	1·04	7·38
				Slow strain				
18	3	225	91·26	0·20	200	112·21	0·33	20·95
	9	98	111·64	0·38	83	140·23	0·47	28·59
	14	33	124·82	1·12	26	163·26	1·23	38·44
23	3	77	60·30	0·26	72	74·26	0·35	13·96
	9	110	89·94	0·29	93	108·31	0·38	18·37
	14	103	98·77	0·30	78	118·35	0·44	19·58
	21	25	109·36	0·40	15	128·67	0·71	19·31
30	3	76	45·62	0·24	74	54·04	0·29	8·42
	9	55	50·56	0·33	42	58·14	0·34	7·58
	14	41	55·63	0·41	32	63·44	0·38	7·81
	21	19	90·84	1·01	13	101·54	1·34	10·70

3. *Influence of humidity.*

The influence of the humidity of air on the rate of development has been mainly a matter of conjecture, as is evident from the works of Candura (1928), Voukassovitch (1929), etc. Candura remarked "Quando l' umidita oltrepassà nei recipienti certi limiti, fa ritardare di molto lo sviluppo dell' insetto." Voukassovitch observing normal oviposition by females liberated in a dry atmosphere and normal hatching of eggs as well as pupation of full-grown caterpillars placed in a similar environment, considered dry environments more favourable to the development of this insect. She has entirely ignored larval development, which is the only stage markedly susceptible to the influence of the humidity of the air. Speicher (1931) observed that dry atmosphere and dry food reduced the size and delayed pupation in *Ephestia kühniella*. Tables 4 and 5 clearly show that the rate of development is affected not only by temperature but also by S.D. of the air. The influence of S.D. is more marked on the larvae and pupae than on the eggs. High S.D., like low temperature, retards development, low S.D. favours it.

In these experiments two sources of error need a special mention. In the first place, no attempt has been made to eliminate the influence of heredity. *Ephestia kühniella* is a rather slow developing insect, and it was not within the scope of present work to breed a number of pure line generations to separate the fast and the slow strains. However, such a possibility does not seem to be remote, and an attempt in this line would lead to a better and more precise understanding of the differences in the two strains.

Food also affects the rate of development quite appreciably. Though the quality of food remained the same in all the experiments, equal amounts were not given. As a matter of fact, the layer of food in dishes was kept as thin as possible with a view to ensuring proper effect of the S.D. of the air on the insects, which usually remain below the layer of food. The food was added from time to time. Since the development of larvae is considerably retarded by lack of food, it is not improbable that in trying to ensure full effect of the humidity of the air, this error may have crept in. Allowance must, therefore, be made for these errors.

Table 6. *The number of generations in a year*

Temp. °C.	S.D. mm.	Pre-imaginal period		No. of generations	
		Fast strain	Slow strain	Fast strain	Slow strain
18	3	82·1	123·4	4·4	3·0
	9	94·8	151·7	3·8	2·4
	14	109·6	175·8	3·3	2·1
23	3	57·3	80·8	6·4	4·5
	9	75·5	115·1	4·8	3·2
	14	86·6	125·4	4·2	2·9
	21	97·7	135·7	3·7	2·7
30	3	36·0	58·0	10·1	6·2
	9	39·2	62·6	9·3	5·8
	14	43·3	68·1	8·4	5·4
	21	70·8	106·5	5·1	3·4

4. *Number of generations.*

The pre-imaginal period and the number of generations of the two strains are given in Table 6. Depending on the environmental conditions, two to six generations of the slow strain and three to ten generations of the fast strain are possible in a year within a range of 18–30°C.

(*d*) *Mortality and reproductive potential*

Mortality.

The eggs of *Ephestia kühniella* are highly resistant to environmental conditions. The viability of fertile eggs (Table 7) is very little affected by temperature or humidity, the percentage of eggs hatching varying between 75 and 85 only. The eggs can hatch out in absolutely dry atmosphere as well as in almost saturated air. Norris also noted this resistance of eggs to environmental conditions; it led Voukassovitch to generalise about the great resistance of this insect to humidity and drought. On the other hand, the rate of mortality during the larval and pupal stages is greatly affected by temperature and more so by S.D. of the air. Table 8 shows that 75–90 % of the larvae reach the adult stage when S.D. is low, while only a small percentage can do so if the S.D. is high.

Table 7. *The percentage viability of fertile eggs under different conditions*

Temp. °C.	S.D. mm.	No. of fertile eggs	No. of larvae hatched	% viability
18	3	1224	1031	84·2
	9	1391	1146	82·4
	14	1105	824	74·6
23	3	2141	1837	85·8
	9	1737	1424	82·0
	14	1645	1193	72·5
	21	1720	1161	67·5
30	3	1122	843	75·1
	9	1372	1047	76·3
	14	1015	751	74·0
	21	2015	1360	67·5
	32	1518	1034	68·1

Table 8. *The percentage mortality during the larval and pupal periods*

Temp. °C.	S.D. mm.	No. of freshly hatched larvae	No. of moths obtained	% mortality
18	3	625	530	15·2
	9	450	289	35·8
	14	240	88	63·4
23	3	460	427	7·2
	9	660	470	28·8
	14	740	296	60·0
	21	220	63	71·4
30	3	430	325	24·4
	9	325	231	28·9
	14	300	112	62·7
	21	250	32	87·2
	32	600	1	99·9

The reproductive potential.

According to Thompson (1922) the reproductive potential of an insect is represented by the product of sex ratio of the adults and the number of progeny produced at each reproduction. The effective reproductive potential must, however, take into consideration the effective sex ratio, or in other words, the number of fertile eggs produced per female, and the mortality during the pre-imaginal stage. This data is presented in Table 9. The effective reproductive potential is highest at a S.D. of 3 mm. at all the temperatures, and a temperature of 23° C. is more favourable than either 18 or 30° C.

Table 9. *The effective reproductive potential of* Ephestia kühniella *under different conditions*

Temp. °C.	S.D. mm.	No. of fertile eggs per female	% viability of eggs	No. of larvae hatched	% larval and pupal mortality	No. of moths	Effective reproductive potential*
18	3	169	84·2	142	15·2	120	64·80
	9	149	82·4	123	35·8	79	42·66
	14	97	74·6	72	63·4	26	14·04
23	3	182	85·8	156	7·2	145	78·30
	9	176	82·0	144	28·8	103	55·62
	14	160	72·5	116	60·0	46	24·84
	21	113	67·5	76	71·4	22	11·88
30	3	82	75·1	62	24·4	47	25·38
	9	45	76·3	34	28·9	24	12·96
	14	24	74·0	18	62·7	7	3·78

* A sex ratio of 54 % females has been used (after Payne, 1933).

4. The biology of *Nemeritis canescens* in controlled environments

(*a*) *General*

Nemeritis canescens is as cosmopolitan as the Mediterranean flour moth, and is almost as regular a visitor of flour mills as its host, but, with the exception of Beling's work (1932) under natural conditions, comparatively very little is known of its life history, much less of its efficiency as a biological check on the host.

The parasite breeds parthenogenetically, and in the course of the present investigation, covering several thousands of individuals, no male was ever met with. Males of this species, however, have been recorded by Dautert-Willimzick (1931) and Beling (1932).

Nemeritis, being an endoparasite, lays its eggs in the body of the host larvae, in whose body fluids the larvae remain till they are full fed and ready to pupate. On account of this characteristic habitat, the S.D. of the air has no direct influence on the pre-imaginal development of the parasite. For this reason only temperature effects are recorded. The longevity of the adults has been investigated at constant temperatures as well as S.D.

(*b*) *Pre-oviposition period*

Wojnowskaja-Krieger (1927–8) mentions that first oviposition takes place on the second or third day after emergence. Candura (1928) also places the pre-oviposition period at "a few days". On the other hand, Beling (1932) and I have observed that females are ready to oviposit immediately after emergence.

(*c*) *Fecundity of females*

In the ovaries of freshly emerged females Wojnowskaja-Krieger counted 280–300 eggs. The actual number of progeny per female, however, is much smaller. This is partly due to superparasitism and partly to the fact that she never lays all the eggs in the ovaries. Normally, a single egg is laid at each sting, but as the parasite cannot distinguish a parasitised host from an unparasitised host, it may sting the same host several times and thus deposit several eggs in the body of the same individual. Wojnowskaja-Krieger observed 15 eggs laid in the body of a single caterpillar, and Beling noticed 27 parasite larvae and 3 parasite eggs in one host larva. But although a number of eggs may be laid in a host, only one parasite emerges successfully. This is due to competition among the newly-hatched parasite larvae resulting in the survival of the strongest. In view of this, the actual number of progeny obtained is the only reliable index of the reproductive potential of the parasite. No attempt has, therefore, been made to study the egg-laying power of the parasite, attention being paid only to the progeny or the number of young emerging as adults. Beling obtained a maximum progeny of 36 from one female; she did not obtain the figure of 75 recorded by Wojnowskaja-Krieger. In my experiments a progeny of about 60 individuals was quite common, and in one case at 23° C. 75 adult parasites were obtained from a single female.

The number of progeny is affected by several factors, of which the following will be considered here:

1. *Effect of the number of host larvae.*

Superparasitism can be reduced, though not eliminated, by increasing the number of host larvae. Experiments were conducted in which 20, 50, 100, 200 and 300 full-grown larvae were offered to a parasite in glass dishes of uniform size (4 in. wide and 2·25 in. deep) at different constant temperatures. Honey solution was supplied to the parasites in each case. The results are presented in Table 10 and Fig. 1.

The number of progeny per female rises with the increase in the number of host larvae to a certain point (100–200 larvae in this case); beyond this, there is no increase even with further increase in the number of the host. It may be pointed out, however, that under natural conditions, where the parasite has unrestricted sphere of movement there are very remote possibilities of the same host larva being stung a number of times. Consequently

a still higher figure would be expected, provided, of course, the host larvae are fairly abundant.

Table 10. *Progeny (which emerged as imagines) per female with different number of host larvae at constant temperatures*

No. of host larvae	18°C.		23°C.		27°C.		30°C.		Mean progeny
	No. of obs.	Progeny	No. of obs.	Progeny	No. of obs.	Progeny	No. of obs.	Progeny	
20	10	6·8	9	8·0	9	6·3	9	6·2	6·8
50	10	11·6	10	24·3	10	16·0	8	17·6	17·4
100	5	38·4	8	32·6	7	24·7	8	19·5	27·9
200	8	40·7	8	36·0	9	32·0	8	31·4	34·9
300	9	37·0	10	38·7	8	31·1	9	34·0	35·4

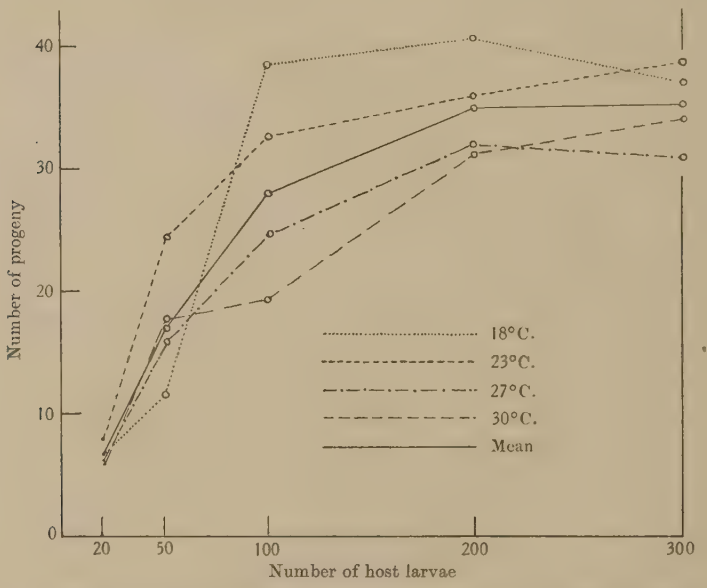

Fig. 1. Progeny per female with different number of host larvae at constant temperatures.

2. *Effect of temperature.*

The production of eggs in the ovaries is influenced by temperature. But the influence of other factors from the time of production of eggs in the ovaries till the emergence of a new generation is so great and so variable in this case, that a small variation in the production of eggs in the ovaries, brought about by temperature, is not manifested in the actual number of progeny produced, i.e. its effective reproductive potential. The number of progeny per female at different constant temperatures is shown in Table 11. There is considerable variation in the individual values even under similar conditions of breeding. Beling also expressed this view.

Table 11. *Progeny of 43 females at constant temperatures each with 300 host larvae*

	15° C.	18° C.	23° C.	27° C.	30° C.
	3	39	67	69	39
	3	43	44	23	25
	4	37	31	24	33
	2	38	27	21	61
	2	63	32	36	26
	5	30	23	31	30
	4	22	29	26	26
	—	24	75	19	27
	—	38	25	—	39
	—	—	34	—	—
Mean	3·3	37·1	38·7	31·1	34·0
Standard error	0·42	4·01	3·70	5·3	3·8
Maximum	5	63	75	69	61

t for mean progeny at 23 and 27° C. (i.e. between the maximum mean and minimum mean) = 1·101 (insignificant).

From the mean figures (Table 11), it will be noticed, there is an indication of slightly higher fecundity at 18 and 23° C., but statistically these differences are not significant. At 15° C. the number of parasites produced is greatly reduced. Whether this is due to a smaller egg production, lack of normal movements of the parent parasite, or a high mortality during the pre-imaginal development, or all acting together, was not determined, but it seems probable that extreme sluggishness noticed at this temperature is the main cause.

3. *Effect of feeding.*

Soon after emergence the females are ready to lay eggs. Feeding the adults on honey, to which I shall refer again, prolongs the imaginal life, but seems to have little effect on the number of progeny produced. Results of some experiments, with and without feeding at three different temperatures, are given in Table 12. The number of progeny in the experiments with feeding is somewhat higher than that in the experiments without feeding, but the difference is again statistically insignificant. In order to analyse the daily rate of oviposition, in one set of experiments the parasites were transferred to a fresh supply of 200 host larvae every day. The results are given in Table 13.

Table 12. *Progeny per female with and without feeding at* S.D. 0 *mm.*

		18° C.		23° C.		27° C.	
Treatment	No. of host larvae	No. of females	No. of progeny	No. of females	No. of progeny	No. of females	No. of progeny
Fed	200	8	40·7 ± 5·8	8	36·0 ± 5·9	9	32·0 ± 4·4
Not fed	200	8	36·4 ± 4·2	10	35·9 ± 3·6	8	26·6 ± 4·5
Fed	300	9	37·0 ± 4·0	10	38·7 ± 3·7	8	31·1 ± 5·3
Not fed	300	8	39·0 ± 4·7	9	33·0 ± 4·8	7	31·0 ± 4·1

t for mean progeny with feeding and without feeding at 27° C., with 200 host larvae = 0·86 (insignificant).

Table 13. *Progeny of* Nemeritis canescens *with and without food at* 23° *C. and* 0 *mm.* S.D. (200 *host larvae supplied daily*)

Days after emergence	A. With honey feeding					B. Without food			
	1	2	3	4	5	1	2	3	4
1	14	9	5	10	12	15	49	15	67
2	4	8	5	7	26	8	5	11	3
3	6	4	2	7	9	14	2	13	3
4	4	4	3	8	4	—	2	—	2
5	5	0	3	4	2	—	—	—	—
6	0	2	3	0	1	—	—	—	—
7	2	1	0	3	1	—	—	—	—
8	2	3	2	2	2	—	—	—	—
9	0	2	2	3	2	—	—	—	—
10	0	0	0	3	3	—	—	—	—
11	0	2	0	0	1	—	—	—	—
12	2	2	2	7	-	-	-	-	-
13	4	1	3	1	—	—	—		—
14	0	0	0	2	—	—	—	—	—
15	0	0	0	0	-	—	—	-	-
16	6	1	2	1	—	-	-	-	—
17	4	2	4	—	—	-	-	—	—
18	0	0	1	—	—	—	—	—	—
19	0	0	4	—	—	—	—	—	—
20	0	0	0	—	-	.	—	-	—
21	0	1	1	—	—	—	-	-	—
22	4	0	—	—	—	—	—	—	—
23	0	1	—	-	—	—	—	-	-
24	3	-	—	—	—	.	—	—	—
25	3	—	—	—	—	—	—	—	
Total progeny	63	43	42	58	63	37	58	39	75
Life of female (days)	31	34	36	17	12	3	4	3	4

A study of these two tables illustrates the following points: (1) The total number of progeny is not appreciably affected by feeding. As a matter of fact the maximum progeny of 75 individuals was obtained from a female kept without food. (2) The largest number of eggs is usually laid during the first few days. (3) When fed, the females seem to withhold their eggs and lay them in a well-distributed manner over the whole imaginal life.

The withholding of eggs referred to above is useful for the preservation of the species. When food is available, egg-laying is spread over as long a period of the parasite's life as possible, and when food is lacking, the maximum number of eggs is deposited within the limited life of the parasite.

(*d*) *Rate of development*

Great confusion exists with regard to the pre-imaginal development of the parasite. This is natural, because almost all investigators have recorded observations from breeding under uncontrolled environmental conditions. Following are some of the figures obtained by previous workers (Table 14).

Observations were carried out on the duration of pre-imaginal period at constant temperatures of 12°, 15°, 18°, 23°, 27°, 30° and 33° C. The parasite

Table 14. *The duration of pre-imaginal development (the period from the time of oviposition to the emergence of adults), according to different workers*

Name of author	Duration days	Temperature
1. Krüger (1921)	49–74	Cold winter
	21	Warm weather
2. Wojnowskaja-Krieger (1927–8)	18–34	20–25° C.
3. Whiting (1928)	27–48	—
4. Candura (1928)	21	—
5. Diamond (1929)	18–26	16–20° C.
6. Daviault (1930)	47–63	18–20° C.
	27–30	28° C.
7. Beling (1932)	28–42	18–22° C.

could not complete its development at 12° or at 33° C. The results are given in Table 15. The pre-imaginal period varies from 103 days at 15° C. to 21 days at 30° C. Time-temperature and temperature-rate curves are shown in Fig. 2. The line of index of development is quite straight except at the upper limit, where a slackening in the rate of development is indicated.

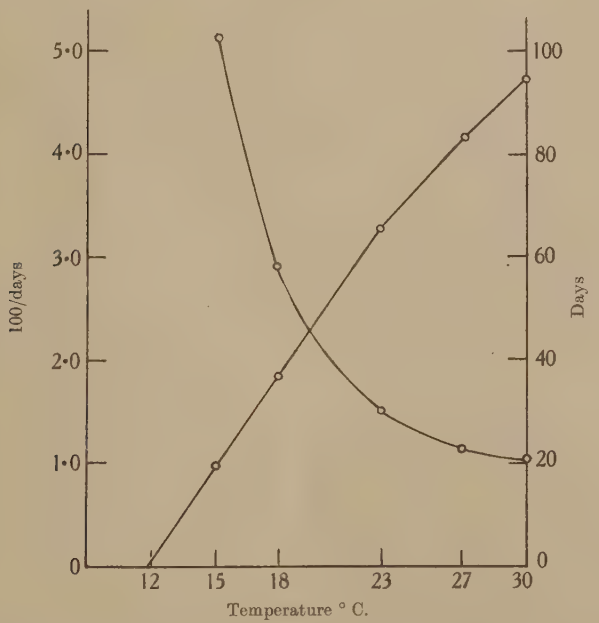

Fig. 2. Time-temperature and temperature-rate curves of the pre-imaginal period of *Nemeritis canescens*.

Table 15. *The pre-imaginal period of* Nemeritis canescens *at different temperatures*

15°C.		18°C.		23°C.		27°C.		30°C.	
No. of days	No. of individuals	No. of days	No. of individuals	No. of days	No. of individuals	No. of days	No. of individuals	No. of days	No. of individuals
81	1	46	1	28	21	22	50	19	1
95	2	48	2	29	211	23	129	20	98
100	3	50	9	30	145	24	117	21	140
102	5	52	41	31	120	25	20	22	57
110	1	54	57	32	41	26	3	23	4
113	1	56	11	33	16	27	4	24	4
117	2	58	7	34	5	—	—	25	7
—	—	60	7	35	2	—	—	26	1
—	—	62	6	36	1	—	—	27	1
—	—	64	3	37	1	—	—	—	—
—	—	66	2	—	—	—	—	—	—
—	—	68	2	—	—	—	—	—	—
—	—	70	5	—	—	—	—	—	—
—	—	72	3	—	—	—	—	—	—
—	—	74	2	—	—	—	—	—	—
Total no. of parasites: 15		158		563		323		313	
Mean duration (days): 102·5		55·5		30·06		23·41		21·05	
Standard error: 2·37		0·31		0·003		0·0027		0·0036	

(e) *Longevity of adults*

1. *Without food.*

Without food, *Nemeritis* adults are very short-lived. The adult life is affected both by temperature and s.d. This is illustrated by Table 16 and Fig. 3.

Table 16. *Longevity of adults at different temperatures and* s.d., *without honey and hosts*

	Longevity in days at different s.d.											
	0 mm.		3 mm.		9 mm.		14 mm.		21 mm.		32 mm.	
Temp. °C.	*1	2	1	2	1	2	1	2	1	2	1	2
0	61	13·2	—	—	—	—	—	—	—	—	—	—
5	73	17·0	51	16·0	—	—	—	—	—	—	—	—
12	51	9·0	64	8·7	—	—	—	—	—	—	—	—
14·5	70	7·6	62	7·5	61	7·0	—	—	—	—	—	—
19	50	5·5	49	5·0	45	4·9	57	4·2	—	—	—	—
23	73	4·0	64	3·7	42	3·5	49	3·3	43	2·8	—	—
27	48	3·0	48	2·7	48	2·4	42	2·3	48	1·9	—	—
30	51	2·4	39	2·3	37	2·2	40	2·0	39	1·6	36	1·4
33	46	2·0	46	1·7	42	1·6	—	—	33	1·4	41	1·25

* 1 stands for number of adults; 2 stands for period (days).

At 33°C. they live only 2 days. The longevity increases as the temperature falls, till the maximum average life of 17 days is reached at 5°C. Further fall in temperature is injurious to the adults, and at 0°C. the average duration is

13 days. It will be noticed, however, that the parasite is considerably resistant to low temperatures. The maximum life is 27 days at 5° C., and 17 days at 0° C. With regard to the humidity of the air, moist conditions seem more favourable to the parasite. The life of the parasite increases with a fall in the S.D. (Fig. 3).

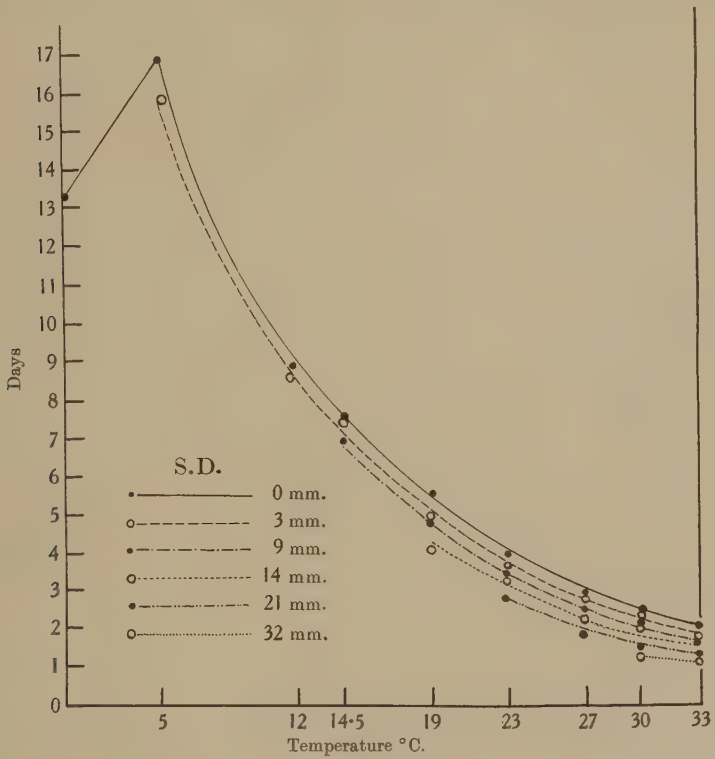

Fig. 3. The longevity of *Nemeritis* adults kept without food at different temperatures and S.D.

Beling failed to keep adults alive longer than 7 days at 0° C., though she had them alive up to a maximum of 24 days at 5° C. But at 0° C. it is difficult to distinguish by sight the living individuals from the dead ones. Even the movement of antennal tips, which is usually maintained up to the point of death, entirely disappears after a few days' exposure to 0° C. Some of the preliminary experiments were actually discontinued through mistaking the motionless parasites for dead ones. Later on, however, the tubes were warmed for 5–10 min. daily, and correct observation recorded after watching body movements, which the living parasites manifested. This behaviour may have been the cause of Beling's low figures.

2. *With food but in the absence of hosts.*

If the adults are fed on honey or sugar solution their life is considerably increased. Figures obtained by previous workers are given below:

Wojnowskaja-Krieger ...	16 days
Diamond	54 „
Candura	50 „
Beling	57 days on sugar solution
	72 days on honey solution

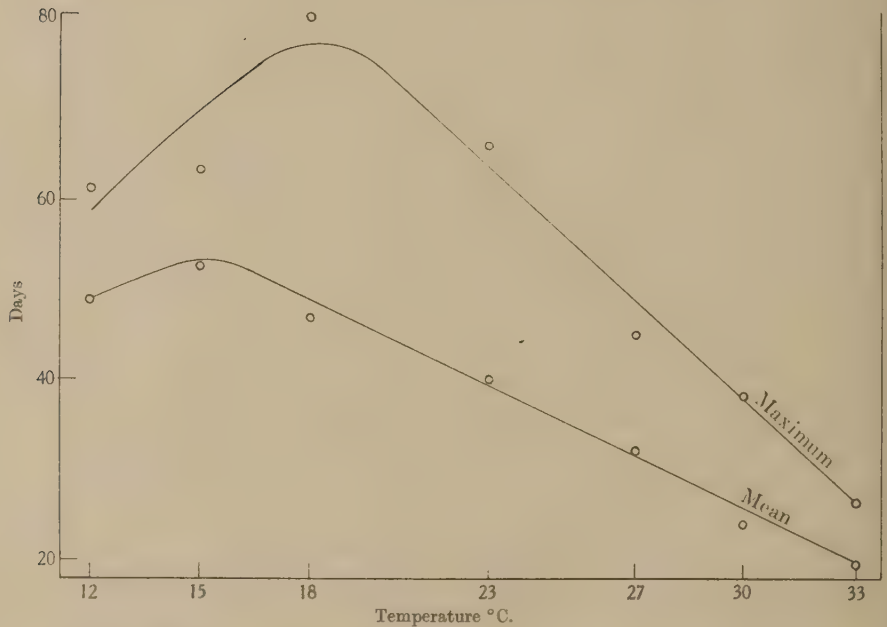

Fig. 4. The longevity of *Nemeritis* adults fed on honey, at 0 mm. s.D. in the absence of the host.

Daviault (1930), on the other hand, states that the life of *Nemeritis* females is 3–4 days without food and "a little longer" when fed on sugar solution. Diamond (1929) maintains that he kept *Nemeritis* alive for 48 days on water. Evidently the former worker did not maintain a proper supply of food, and the latter might have used sugar solution instead of water, because *Nemeritis* adults live no longer on water than without it. Longevity of the parasite in days at different temperatures when fed on honey solution is shown in Table 17 and Fig. 4. The average duration goes on increasing with a decrease in temperature, till the maximum mean is reached at about 15° C. Further fall in temperature reduces the adult life. The maximum life was 80 days at 18° C.

Table 17. *The longevity of adults by feeding on honey at* S.D. *of* 0 *mm. and different constant temperatures (without the host)*

Temp. °C.	No. of adults	Longevity in days	
		Maximum	Mean
12	8	61	49
15	37	63	53
18	59	80	47
23	24	66	40
27	24	45	31·7
30	28	38	24
33	25	26	19

3. *With food but in the presence of host.*

Though the life of the adults when fed is somewhat shorter in the presence of host than in their absence, the effect is not appreciable. Beling, however, mentions that the parasite could not live more than 7 days in spite of feeding, in case the host larvae were supplied.

In view of the observations recorded in Table 18, it is difficult to understand why Beling failed to keep the parasites longer. The maximum life was 66 days at 18°C. It was also noticed in other experiments that quite a number of parasites yielding a progeny of 59–63 individuals lived as long as 38 days when fed.

Table 18. *The longevity of adults with honey feeding and with host at different temperatures* (S.D. 0 *mm.*)

Temp. °C.	No. of adults	Mean longevity days	Maximum longevity days
18	41	31·6	66
23	31	20·0	29
27	26	20·6	31
30	29	18·0	23

A small reduction in the average longevity in Table 18 as compared to that without the host shown in Table 17, may be due to some exhaustion brought about by the heavy duties of oviposition. This is further supported by the fact that females kept with the host larvae for 48 hours without food (thus having laid a large portion of their eggs, *vide* Table 13) and then fed on honey in the absence of host, lived a comparatively shorter life (Table 19).

Table 19. *Longevity of* 61 *adults at* 23°*C. and* S.D. *of* 0 *mm. with honey feeding after ovipositing for* 48 *hours on the host*

Longevity (days)	No. of adults
1	20
3	18
4	8
7	2
12	8
15	4
54	1

(*f*) *Heliotropic response of adult parasites*

It is a matter of common observation that the freshly emerged parasites are strongly attracted to light. Beling quotes some interesting observations from her experience of the parasite under natural conditions. She observed that *Nemeritis* spent a part of its life outside the mills, the breeding place of its host. On the one hand, she found a large number of adults collecting on the glass windows of mills trying to find their way out; on the other hand, those found in the open were coming back to the mills. She thought that perhaps the parasite was able to feed on the nectar of flowers in the open, because she observed that returning individuals were carrying drops of honey in their mouths. The significance of a considerable prolongation in the life of the adults by feeding under natural conditions has been the subject of several conjectures. Krüger (1921) thought that in mills the fermenting flour in moist places may be hydrolysed and used as food. Diamond (1929), however, maintained that the parasite could not utilise any of the mill products.

This view is substantiated by Beling's observations quoted above, but, owing apparently to positive and negative heliotropic responses involved in her observations, she concluded that, pending further investigation, nothing could be said definitely of the probability of the parasite being able to feed under natural conditions.

It will be observed that in order to establish the possibility of feeding under natural conditions, two quite opposite phases in the life of the adult parasite must be recognised. With a view to feeding, the parasite must abandon its dark habitat in the mill and go out in the open, i.e. it must be positively heliotropic. Having satisfied its food requirements it must return to the mills in search of its host, to oviposit and perpetuate its species, i.e. it must become negatively heliotropic. These two habits must alternate throughout the adult life of the parasite. To prove this hypothesis the following experiment was carried out: Three pieces of glass tube with a bore of 1 in. were fitted end to end on a wooden board. The length of the middle piece was 6 in., that of the pieces on either side was 12 in. The joints between the three tubes and also the outer ends were fitted with thin partitions which could be put in or drawn out as needed. The entire tube was covered with a thick black cloth. One end of the apparatus was always kept dark, the other could be illuminated from daylight by a glass slide. 20 parasites were liberated each time in the central compartment and the entire apparatus was kept dark for 30 min. Light was then turned on at one end and the two partitions on either side of the middle compartment drawn out. The number of parasites in each compartment was recorded after known intervals. Series of experiments were carried out with freshly emerged, starving, and full-fed individuals. It will suffice to quote here one of these, as the results of all were identical (Table 20).

Table 20. *Heliotropic response of parasites*

Exp. No.	No. of observation	Time of observation hr.	min.	No. of parasites in each compartment: Lighted	Middle	Dark	Remarks
1	(1)	10	0	0	20	0	Started with freshly emerged parasites enclosed in the middle compartment
	(2)	10	30	—	—	—	Light turned on and partitions removed
	(3)	10	30½	14	6	0	—
	(4)	10	34	18	2	0	Parasites fed on honey from 10.34 to 11.0 and experiment repeated
2	(1)	11	0	0	20	0	
	(2)	11	30	—	—	—	Light turned on and partitions removed
	(3)	11	30½	0	0	20	—
	(4)	11	35	0	1	19	Parasites left without food in middle compartment for 24 hours and experiment repeated
3	(1)	11	30	0	20	0	
	(2)	11	30	—	—	—	Light turned on and partitions removed
	(3)	11	30½	12	4	4	—
	(4)	11	34	13	5	3	Parasites left for another 24 hours in the central compartment and experiment repeated
4	(1)	11	30	0	20	0	
	(2)	11	30	—	—	—	Light turned on and partitions removed
	(3)	11	30½	20	0	0	—
	(4)	11	34	20	0	0	—

These experiments establish beyond doubt that the freshly emerged parasites are positively heliotropic, that after feeding they become negatively heliotropic, and that again when starved they are attracted to light. These observations offer a very clear explanation of what Beling supposed might take place under natural conditions.

5. HOST-PARASITE BALANCE

From the individual study of the host and parasite under known environments very reliable conclusions can be drawn in regard to the influence of these factors on the host-parasite balance.

(*a*) *Reproductive potential*

The reproductive potential of the host is markedly affected both by temperature and S.D. of the air; that of the parasite is influenced neither by S.D.

Table 21. *The reproductive potential of host and parasite*

Temp. °C.	S.D. mm.	Reproductive potential of host	Reproductive potential of parasite
15	—	42·1*	3·3
18	3	64·8	37·0
	9	42·7	
	14	14·0	
23	3	78·3	38·7
	9	55·6	
	14	24·8	
	21	11·9	
30	3	25·4	34·0
	9	13·0	
	14	3·8	
	21	0·0	

* Quoted from Payne (1933).

nor to any appreciable extent by temperature. Table 21, showing the reproductive potential of the host and parasite under different combinations of temperature and S.D., illustrates this point. At a temperature of 30°C. the reproductive potential of the parasite is greater than that of the host; at this temperature the parasite would always be able to overtake the host. At temperatures of 18 and 23°C. the reproductive potential of the host is greater than that of the parasite when the S.D. is 9 mm. or less; but it is lower than that of the parasite when the S.D. is higher than 9 mm. At 15°C. the reproductive potential of the parasite falls very low, so that there is no possibility of its overtaking either strain of the host.

(*b*) *Rate of development*

The development of the host is affected by temperature as well as by S.D., that of the parasite only by temperature; S.D. having no direct effect, because the most sensitive stage of the parasite's development is passed within the body fluids of the host. Comparing the duration of development of the host and its parasite under different environmental conditions, we get Table 22. At 23°C. the parasite is able to complete two generations with one of the host at almost all the S.D., and would therefore be able to annihilate the fast as well as slow strains of the host. At 18°C. the parasite can complete two generations with one generation of the slow strain of the host only, therefore it can overtake the slow strain. At 15°C. both low reproductive potential and slow development go against the parasite. The threshold of development of the host lies between 8° and 10°C., that of the parasite between 12° and 15°C. Below 15°C. the host can carry on its development, the parasite cannot.

Table 22. *The pre-imaginal period of host and parasite*

Temp. °C.	S.D. mm.	Pre-imaginal period of the host days		Pre-imaginal period of the parasite days
		Fast strain	Slow strain	
15	—	85–90*	135–157*	103
18	3	82	124	55·5
	9	95	152	
	14	110	175	
23	3	57	81	30
	9	76	115	
	14	87	125	
	21	98	136	
30	3	36	58	21
	9	39	63	
	14	43	68	
	21	71	105	

* From Payne's data (1933).

Thus the study of the available data leads to the conclusion that at temperatures of 23°C. and above, the parasite is stronger than the host; between 15° and 23°C. the parasite can overtake only the slow strain of the host. At

15°C. and under, the parasite can compete with neither strain of the host. High S.D. acts against the host, but has no direct influence on the parasite.

(c) *Other factors*

The parasitisation of the host is limited to a definite stage of its development, viz. the last larval and early pupal stages. This fact favours the host, since a host with a regular rate of development has a great possibility of placing the parasite in a periodical difficulty of finding suitable stages. But *Ephestia kühniella*, in possessing a mixture of strains with a wide range in their rates of development and a consequent overlapping of broods, offers the regular presence of vulnerable stages. This fact, coupled with the great prolongation in the adult life of the parasite by feeding, favours the parasite.

The host larvae are negatively heliotropic and usually seek darkest places for pupation. To this the parasite has adapted itself by becoming negatively heliotropic after feeding.

The lack of discrimination between unattacked healthy hosts and those already parasitised on the part of the parasite, is favourable to the host. Under natural conditions, however, this obtains only in cases of a high ratio of parasites to host population.

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7. SUMMARY

The reproductive potential and development of *Ephestia kühniella* are adversely affected by high temperature (above 23°C.) and high saturation deficiency (above 14 mm.). Under these conditions the adults exhibit a marked degree of sterility and the larval and pupal stages show a high mortality, but the viability of the eggs is only slightly affected.

Nemeritis canescens being an endoparasite, its reproductive potential is affected neither by S.D. nor appreciably by temperature.

The host possesses two strains. Their threshold of development lies between 8° and 10°C.: that of the parasite between 12° and 15°C. In the absence of food *Nemeritis* adults are only short-lived; by feeding them on honey solution life is considerably prolonged, the maximum being 80 days at 18°C.

At 23°C. and above, both on account of its quicker development and higher reproductive potential, the parasite can overtake the host; at 18°C. and under, the reproductive potential of the parasite falls below that of the host and the rate of development is also greatly reduced: thus high temperature favours the parasite, low temperature favours the host.

While the host is susceptible to parasitisation only during a limited period in development, the mixture of strains prevailing results in the continuous presence of the host in the right condition. The long life of the parasite in the presence of food also carries it over, should there be a temporary scarcity of suitable stage of the host. The parasite is normally positively heliotropic; the host is negatively so. To this the parasite has adapted itself by becoming negatively heliotropic after feeding.

REFERENCES

Beling, I. (1932). "Zur Biologie von *Nemeritis canescens* Grav." Z. Angew. Ent. 19: 223–49.

Brindley, T. A. (1930). "The growth and development of *Ephestia kühniella* Zeller, and *Triobolium confusum* Duval, under controlled conditions of temperature and relative humidity." Ann. Ent. Soc. Amer. 23: 741–57.

Burkhardt, F. (1919). "Zur Biologie der Mehlmotte (*Ephestia kühniella* Zeller)." Z. Angew. Ent. 6: 25–60.

Buxton, P. A. (1931). "Atmospheric humidity in relation to entomological problems." Bull. Ent. Res. 22: 431–47.

Candura, G. S. (1928). "Contributo alla conoscenza della tegnola grigia delle proviste alimentari, *Ephestia kühniella* e del suo parasita, *Nemeritis canescens*." Boll. di Zool. Portici, 21: 149–251.

Chittenden, F. H. (1896). "The development of the Mediterranean flour moth." Bull. Bur. Ent. U.S. Dept. Agric. 6.

Dautert-Willimzick, E. (1931). "Einige Beobachtungen über das bisher unbekannte Männchen der Schlupfwespe *Nemeritis canescens* Grav." Zool. Anz. 93: 274.

Daviault, L. (1930). "Notes biologiques sur *Nemeritis canescens* Grav. et sur la morphologie de ses divers stades." Rev. Path. Vég. Ent. Agr. 17: 82–93.

Diamond, V. R. (1929). "The biology of *Nemeritis canescens*, a parasite of the Mediterranean flour moth." 60th Annual Report Ent. Soc. Ontario, 84–9.

Gierke, E. von (1932). "Über die Häutungen und Entwickelungsgeschwindigkeit der Larven der Mehlmotte *Ephestia kühniella* Zeller." Arch. Entw. Mech. 127: 387–410.

Hase, A. (1924). "Untersuchungen und Beobachtungen über die Gespinste und über die Spinntätigkeit der Mehlmottenraupen *Ephestia kühniella* Zeller." Arb. biol. Anst. Land. Forstw. Berlin, 13: 79–128.

Hase, A. (1927). "Über Temperaturversuche mit den Eiern der Mehlmotte (*Ephestia kühniella* Zeller)." Arb. biol. Anst. Land. Forstw. Berlin, 15: 109–33.

Hefley, H. M. (1928). "Differential effect of constant humidities on *Protoparce quinquemaculatus* Haworth, and its parasite *Winthemia quadrupustulata* Fabricus." J. Econ. Ent. 21: 213–21.

Jakobi, A. (1905). "Die Mehlmotte (*Ephestia kühniella* Zell.)." Kais. Biol. Anst. f. Land und Forst, 16.

Janisch, E. (1933). "Untersuchungen über die Ökologie und Epidemiologie der Nonne. I. Die Abhängigkeit der Entwickelungsdauer von Temperatur und Luftfeuchtigkeit." Arb. biol. Anst. Land. Forstw. Berlin, 20: 269–90.

Kirkpatrick, T. W. (1923). "The Egyptian cotton-seed bug (*Oxycarenus hyalinipennis* Costa)." Bull. Ministry Agric., Egypt, 35: 106 pp.

Krüger, P. (1921). "Beobachtungen am Mehlmottenparasiten *Nemeritis canescens* Grav. Zugleich ein Beitrag zur Kenntnis der äusseren Anatomie der Ichneumoniden." Z. Angew. Ent. 7: 58–67.

Lathrop, F. H. (1923). "Influence of temperature and evaporation upon the development of *Aphis pomi* De Geer." J. Agric. Res. 23: 969–87.

Lund, H. O. (1934). "Some temperature and humidity relations of two races of *Trichogramma minutum* Riley." Ann. Ent. Soc. Amer. 27: 324–40.

Mansbridge, G. H. (1933). "The breeding of *Ephestia kühniella* Zeller in large numbers for experimental work." Ann. Appl. Biol. 20: 771–4.

Menusan, H. (1934). "Effects of temperature and humidity on the life of the Bean weevil, *Bruchus obtectus* Say." Ann. Ent. Soc. Amer. 27: 515–26.

Norris, M. J. (1933). "Experiments on the factors influencing fertility in *Ephestia kühniella* Z." Proc. Zool. Soc. Lond. 4: 903–34.

Parker, J. R. (1930). "Some effects of temperature and moisture upon *Melanoplus mexicanus* Saussure and *Camnula pellucida* Scudder." Bull. Univ. Montana Agric. Exp. Sta. 223: 132 pp.

Payne, N. M. (1933). "The differential effect of environmental factors upon *Microbracon hebetor* Say. and its host *Ephestia kühniella* Z." Biol. Bull. 65: 187–205.

Speicher, B. R. (1931). "The effect of desiccation upon growth and development of Mediterranean flour moth." Proc. Pennsyl. Acad. Sci. 5: 79–82.

Thompson, W. R. (1922). "Théorie de l'action des parasites entomophages. Accroissement de la proportion d'hôtes parasites dans le parasitisme cyclique." C.R. Acad. Sci., Paris, 175: 65–8.

Uvarov, B. P. (1931). "Insects and climate." Trans. Entom. Soc. Lond. 79: 1–247.

Voukassovitch, P. (1929). "Observations biologiques sur un Lepidoptera (*Ephestia kühniella* Zell.)." C.R. Soc. Biol., Paris, 100: 62–4.

Webster, F. M. and **Phillips, W. J. (1912).** "The spring grain aphis or green bug." Bull. Bur. Ent. U.S. Dept. Agric. 110: 153 pp.

Whiting, P. W. (1928). "Biological notes on *Nemeritis canescens*." Psyche, 35: 125–6.

Wojnowskaja-Krieger, T. K. (1927–28). "Zur Biologie von *Nemeritis canescens* G. des Parasiten *Ephestia kühniella* Z." Report of the Bureau of Applied Entomology, vol. 3, Leningrad. (Russian, with German Summary.)

NOMOGRAMS FOR SATURATION DEFICIENCY

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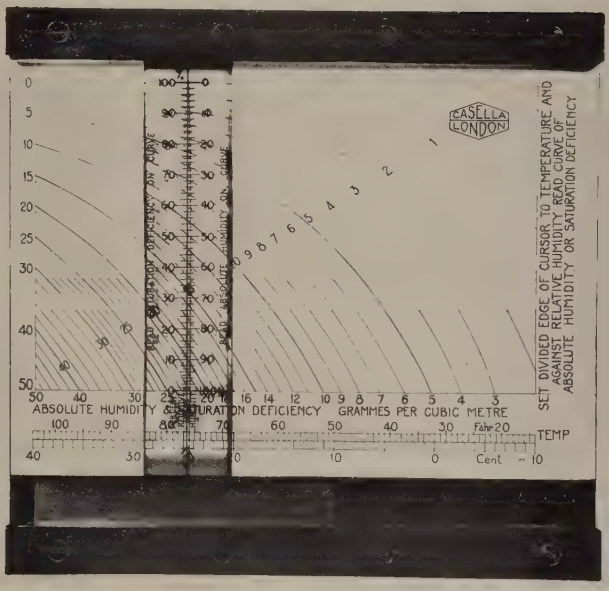
(*With Plate* 2)

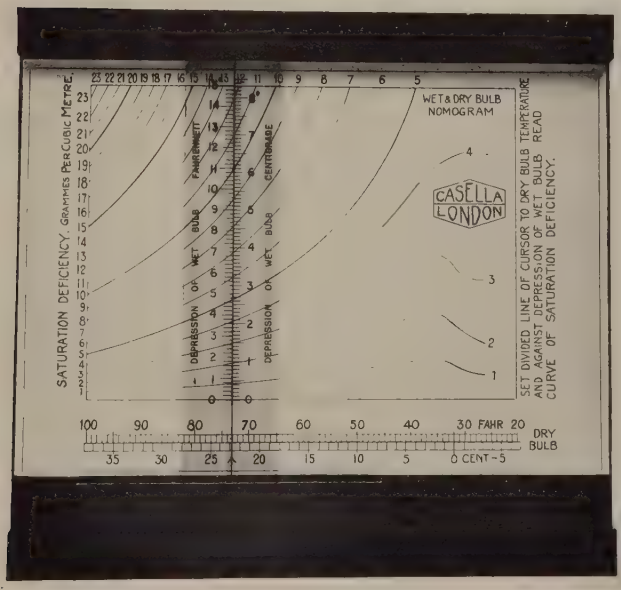
When one measures humidity in ecological studies, it is the drying power of the atmosphere in which one is primarily interested. The expression of atmospheric humidity in terms of saturation deficiency (S.D.)—instead of relative humidity (R.H.)—has the advantage that the figures tend to be proportional to the drying power of the atmosphere, whatever the temperature may be. S.D. may be conveniently expressed in grams per cubic metre (i.e. the number of grams of water that one would have to add to a cubic metre of air to saturate it, the temperature remaining constant). If two lots of air have the same S.D., similar objects will tend to dry at the same rate in both of them, although the temperatures of the two may be different. If one lot has twice the S.D. of the other, similar objects will tend to dry twice as quickly in the first.

The writer has already described (1935) a nomogram by means of which the S.D. of the atmosphere may be rapidly obtained when the temperature and R.H. are known. A simpler form of this nomogram is shown in photo 1. To obtain the S.D., slide the cursor to right or left until the line running along the middle of it cuts the temperature on the scale at the bottom of the nomogram. Both Centigrade and Fahrenheit scales are given. Either the S.D. or the absolute humidity may now be read off on the curves (to the nearest fifth or tenth of a gram, by estimation), from the position of the point on the cursor representing the known R.H. This nomogram is intended for the use of those who already know the R.H. from readings of hair hygrometers or from data given in books. Thus, if one reads in a meteorological report that in a certain place at a certain time the temperature was 65° F. and the R.H. 68 %, one may immediately read off the S.D. as 5·0 gm. per cu. m. This instrument may be called S.D. Nomogram No. 1.

A second type of S.D. Nomogram, No. 2, is shown in photo 2. This is intended for the use of those who wish to use wet- and dry-bulb thermometers and to obtain the S.D. of the atmosphere without calculation and without the use of tables. This nomogram may therefore be called the wet- and dry-bulb nomogram. To use it, slide the cursor to right or left until the line running along the middle of it coincides with the known dry-bulb temperature (C. or F.). The S.D. may now be read off on the curves, from the position of the point on the cursor representing the known depression of the wet bulb (i.e. the number of degrees, C. or F., by which the wet-bulb reading is less than the


CASELLA
LONDON
SET DIVIDED EDGE OF CURSOR TO TEMPERATURE AND AGAINST RELATIVE HUMIDITY READ CURVE OF ABSOLUTE HUMIDITY OR SATURATION DEFICIENCY
ABSOLUTE HUMIDITY & SATURATION DEFICIENCY GRAMMES PER CUBIC METRE
TEMP
Fahr
Cent

Phot. 1. Saturation deficiency nomogram No. 1.


SATURATION DEFICIENCY GRAMMES PER CUBIC METRE
WET & DRY BULB NOMOGRAM
CASELLA
LONDON
SET DIVIDED LINE OF CURSOR TO DRY BULB TEMPERATURE AND AGAINST DEPRESSION OF WET BULB READ CURVE OF SATURATION DEFICIENCY.
DEPRESSION OF WET BULB FAHRENHEIT
DEPRESSION OF WET BULB CENTIGRADE
DRY BULB
FAHR
CENT

Phot. 2. Saturation deficiency nomogram No. 2.

dry-bulb reading). Thus, if the dry-bulb thermometer shows 71°F. and the wet bulb 66°F., the S.D. may be read off as 5·0 gm. per cu. m.

The figures on which the curves for Nomogram No. 2 were based were obtained, by interpolation, from the figures of R.H. given by Glaisher (1930) and Marriott (see Reeves, 1921), and from Messrs Richard's privately printed table of the weight of water contained in a cubic metre of air at various temperatures, which agrees closely with those of other authorities. It will be noticed that the curves are irregular below the temperature at which the density of water is at its greatest.

Glaisher's and Marriott's tables give the R.H. from wet- and dry-bulb readings in still or nearly still air, and the S.D. is only truly given by the nomogram when the wet-bulb thermometer is exposed in still air. However, it is intended that the nomogram shall be used in such a way as to integrate the effect of movements of the air with the effects of the temperature and R.H., in such a way as to give a single figure (index of drying power, or I.D.P.), proportional to the drying power of the atmosphere. To obtain the I.D.P., expose the thermometers to the full draught whose drying power it is intended to measure, and use the wet- and dry-bulb nomogram as before. The figure given will be the I.D.P., and will be proportional to the drying power of the draught. Thus, if one draught gives an I.D.P. of 4 and another gives an I.D.P. of 8, objects will tend to dry twice as rapidly in the second draught as in the first. If the I.D.P. under certain conditions is 8, then objects will tend to dry under those conditions as rapidly as they would dry in still air with a S.D. of 8 gm. per cu. m. When the atmosphere is absolutely still, the I.D.P. and the S.D. will be the same.

It would have been possible to have used tables for ventilated thermometers instead of Glaisher's and Marriott's, and to have relied upon the use of whirling hygrometers or Assmann psychrometers; but if this had been done, the nomogram could not have been used to measure the drying power of a draught. It will be found that with still air the results given by the wet- and dry-bulb nomogram are very nearly the same as those obtained by calculation from readings of the whirled hygrometer used in conjunction with the humidity tables intended for use with it.

The use of the wet- and dry-bulb nomogram is especially indicated whenever the air is in motion, as, for instance, in out-of-doors work in animal or plant ecology, or, again, in large buildings supplied with conditioned air, or in the withering lofts of tea factories supplied with forced draught fans. It is hoped that the optimum I.D.P. for the comfort of workers and audiences and for the proper withering of tea, etc., will be ascertained by experiment; and that thereafter the rate of flow of the atmosphere will be increased or decreased until the proper I.D.P., as shown by the nomogram, is attained.

The two nomograms may be obtained from Messrs C. F. Casella, Regent House, Fitzroy Square, London, W. 1, who will supply with them a simple

table for converting readings in gm. per cu.m. into readings in mm. of mercury, for the use of those who prefer to express S.D. in terms of vapour pressure.

SUMMARY

Simple nomograms are described which give the saturation deficiency (drying power) of the atmosphere, the first from data of temperature and relative humidity, the second directly from wet- and dry-bulb readings.

REFERENCES

Baker, J. R. (1935). J. Sci. Instrum. 12: 214.
Glaisher, J. (1930). "Hygrometrical tables." London.
Reeves, E. A. (1921). "Hints to travellers." London.

DISTRIBUTION OF THE BADGER (*MELES MELES*) AROUND DENBIGH WITH NOTES ON ITS FOOD AND HABITS

By GWION DAVIES

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(*With* 1 *Map in the Text*)

1. Introduction

This survey of badger sets around Denbigh was made in August 1935 and in a week of December 1935. The area searched is shown on the accompanying map, but I cannot profess to have made an exhaustive search personally over the whole area. The country around Denbigh, outside of the Vale of Clwyd, is hilly, well wooded, and watered by numerous brooks; there is a wide extent of moorland in the upper reaches. The farms are dairy and sheep farms, with little arable land. There are nine wooded estates in the survey area, eight of which employ nine gamekeepers.

I have examined 15 occupied sets and 14 deserted sets. A badger's set is generally identified by its large entrance, the smell inside, and the heap of soil, grass and stones outside. It will probably be approached by runs, whilst in the soil around the entrance may be badger hairs. Round about the set may be groups of dung, and occasionally padmarks in any soft mud. The presence of a fox or badger can be tested by placing two upright sticks in the mouth of the set, a little wider apart than the width of a rabbit, or even one stick placed vertically across the hole; the sticks will be pushed aside if a badger comes out, but I have had no experience with a fox. A rabbit burrow is usually smaller, with distinctive smell, but with less excavated soil than a badger set, and often has dung pellets on the threshold. A fox's den in a deserted badger set can be distinguished from the badger's occupied set by its smell and padmarks. Reliable information on other badger sets was obtained from five gamekeepers on whose regular beats four of the sets are, the other two being just outside.

In addition to this census, information has been gathered from gamekeepers and others on the damage supposed to be done by badgers and on the food they eat. The dung has been examined for evidence, though some food, such as worms, may be entirely digestible and leave no traces. The supposed damage done by badgers, no matter how imaginary it may be, is of sufficient importance for discussion in this paper, because the survival of the badger depends partly on farmers' and gamekeepers' notions and knowledge.

In Tables 1 and 2 the descriptions vary in fullness. In all cases where the writer has seen the sets for himself, the height above sea level, configuration, soil, description of vegetation, and gradient are given. The distances from the nearest running water and human habitation are added. The heights above sea level are estimations based on the contour lines on the Ordnance Survey maps.

2. Distribution and descriptions of sets

Table 1. *Occupied sets**

No.	Locality	Height in ft.	Gradient	Soil	Vegetation	Distance from Farm yd.	Distance from Stream yd.
1	Bachegraig	100	Slope	Red sand	Wood	150	350
2	Elwy Bank	200	Slope	Brown sand	Grassy bank	440	100
3	Cefn Rocks	250	Slope	Impregnable set in cave	Wood	400	100
4	Plas Newydd	250	Slope	Red sand	Wood	100	7
5	Plas Heaton	400	Slope	Clay	Wood	100	600
6	Tywysog	500	Bank	Clay and gravel	Wood	400	50
7	Eriviat i	500	Slope	Clay and gravel	Wood	550	300
8	Groes Bach	550	Hedge bank	Clay	Open field	300	5
9	Pandy	400	Slope	—	Wood	—	Less than 50
10	Dolhyfryd	300	Slope	—	Wood	—	Less than 120
11	Ystrad	200	Slope	Brown sand	Wood	350	50
12	Rossa	350	Slope	Clay	Wood	350	10
13	Nant	500	Slope	Clay	Wood	100	15
14	Maes y Plwm	550	Slope	Clay	Thinly wooded field	440	150
15	Y Garnedd Isaf	650	Slope	Clay	Wood	440	440
16	Nant yr Hengoed	480	Slope	Clay	Wood	350	15
17	Nantglyn	900	Bank	Clay	Edge of cornfield	50	150
18	Parc Postyn	500	Slope	—	Wood	—	Less than 90
19	Tyddyn Uchaf	250	Slope	Brown sand	Wood	250	20
20	Nant Goch	300	Slope	Brown sand	Thinly wooded scrub	440	60

* Of the above the writer has examined personally Nos. 1, 2, 3, 4, 6, 8, 11, 12, 13, 14, 15, 16, 17, 19, 20.

For 19 occupied sets the height ranges in 100 ft. stages from about 100 to 650 ft.; one set is 900 ft. up.

Out of 20 sets, 20 are in slopes or banks, 10 in clay, 6 in sand and 17 in woods.

Out of 17 sets, 12 are more than 250 yd. from a farm, and of these, 10 are more than 350 yd. distant.

Out of 20 sets, 16 are less than 150 yd. from a stream.

Table 2. *Deserted sets**

No.	Locality	Height in ft.	Gradient	Soil	Vegetation	Distance from Farm yd.	Distance from Stream yd.
A	Tywysog	550	Slope	Clay	Wood	500	20
B	Tywysog	500	Slope	Clay	Wooded banks of brook	500	1
C	Foxhall	400	Slope	Clay	Wood	500	5
D	Coed Wenci	400	Nearly flat	Clay	Wood	500	50
E	Segrwyd	300	Nearly flat	Clay	Wood	400	30
F	Segrwyd	300	Slope	Clay	Wood	100	30
G	Wood near Caeau Gwynion	300	Trench bank	Clay	Wood	300	10
H	Segrwyd Uchaf	500	Slope	Clay	Wood	300	10
I	Wood by Aberglyniau	600	Hedge bank	Clay	Wood	100	10
J	Y Garnedd Isaf	650	Slope	Clay	Wood	500	440
K_1 K_2	Y Garnedd Uchaf	700	Slope	Clay	Wood	300	10
L	Near Nant	500	Bank	Clay	Edge of field	300	350
M	Ty'n y Ffynon	700–1000	—	—	—	—	—
N	Gwaenynog Bach	500	Bank	Sand	Sandpit in open field	440	250
O	Eriviat ii	500	Slope	Clay	Wood	250	5

* Of the above the writer has examined all but M.

For 16 deserted sets the height ranges in 50–100 ft. stages from 300 to 750 ft. (approximately).

Out of 16 sets, 12 are in slopes or banks.

14 are in clay.

12 are in woods.

13 are more than 250 yd. from a farm, 5 of these being over 500 yd. away.

12 are less than 50 yd. from a stream.

All but four of the badger sets are in woods or close to their outskirts. Since the countryside is hilly it is hard to tell whether the reason that all the badgers have their sets in a hillside or bank is that of choice or compulsion; the absence of badgers from flat places is weak evidence. Similarly, since 10/20 of the occupied, 14/16 of the deserted sets are in clay soil, it is hard to tell whether the clay soil, or other factors, decided the site of the set; yet, it seems as if the badger is better able to avoid being dug out in sandy soil than in clay. The fact that 16/20 of the occupied and 12/16 of the deserted sets are less than 150 yd. from a stream may be due to the fact that most of the woods follow the river valleys, but the same thing may be true of the badger's occurrence in woods, considering that most of the river valleys to the south and west of Denbigh are wooded. The fact that 12/20 of the occupied sets are more than 250 yd. and 10/20 more than 350 yd. from a farm may be due to chance or it may be that the farms are avoided by the badger; in that case it is interesting to note that 13/16 of the deserted sets are more

than 250 yd., and 7/16 more than 400 yd. from a farm. The apparent absence of badger sets from the moorlands may be due to the unsuitability of the soil,

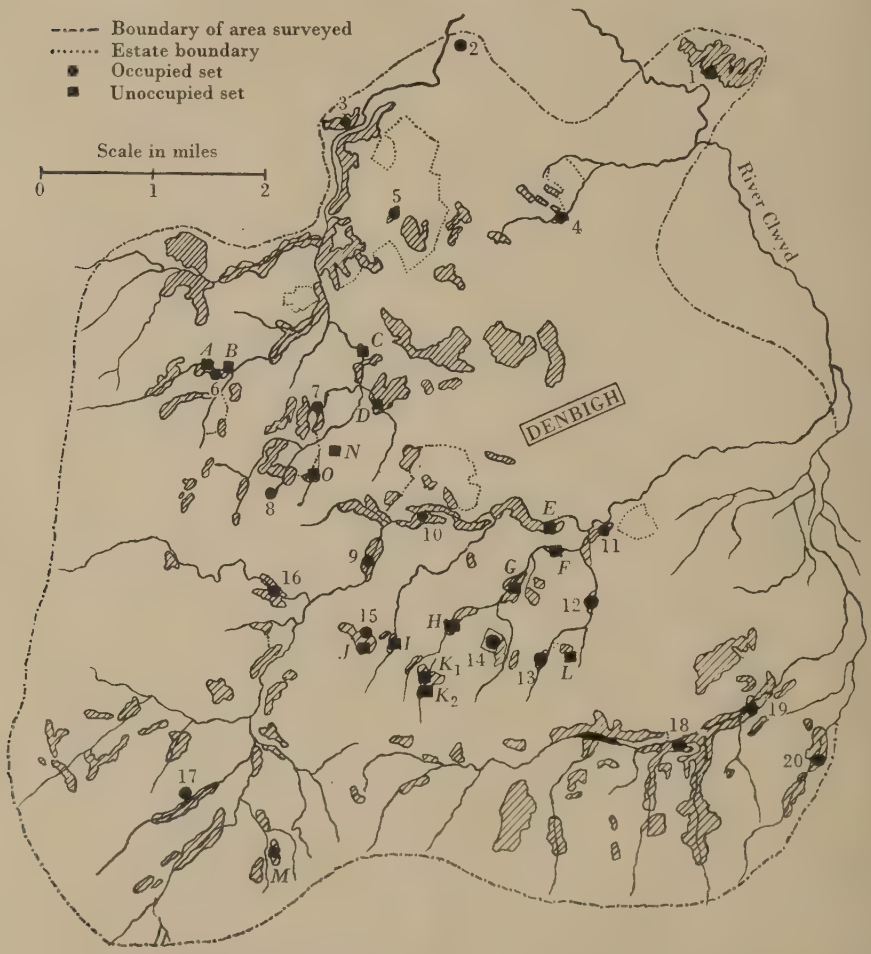

Fig. 1. Map of the Denbigh district showing the distribution of badger sets in the area surveyed.

climate and physical features of the moors for supporting the badger itself, or the flora and fauna upon which the badger seems to depend. It is well to note that even though the badger seems to be difficult to trap with a spring trap, persecution was a limiting factor in set C.

3. Food

Analysis of dung. This was done in April, August and December 1935, and the results seemed to vary according to seasonal food available. In each lot of dung the hair of rabbits (*Oryctolagus cuniculus*) and the undigested remains of dorbeetles (*Geotrupes stercorarius*) were conspicuous. In the April sample there was a fragment of the scaly skin of a small bird's foot, and a quantity of finely broken fragments of small lower jawbones with teeth, 11 and 16 mm. long, as well as the incisor teeth, of very young rabbits. In the August sample, a bucketful of which was washed out in a sack, there was a great quantity of dorbeetle remains, three or four larvae skins, a few incisor teeth of very young rabbits, $\frac{3}{8}$ in. of a bird's quill, and a quantity of short rabbit hair. There were other short hairs which could not be identified with confidence. Most of the débris consisted of husks of wheat and oats. In the December sample, 8 lb. of washed dung gathered from four different sets, were mostly vegetable débris and rabbit hair, while acorn shells and dorbeetle remains were conspicuous. There were also the skin off a bird's foot, with toes 18 and 15 mm. long, a bird's quill 14 by 1 mm., about $1\frac{1}{2}$ sq. in. of broken white egg shells of half the thickness of a hen's egg shell, a few splintered bird bones 5 mm. in diameter, and a larva skin.

Other observations on food. Mr Walter Jones, keeper, Garn, shot three badgers returning to their sets at dawn at different times in the spring, and on opening their stomachs he found one full of earthworms, another full of small rabbits from the nest, and the third containing broken pheasants' eggs. It was often stated by gamekeepers that badgers raid the nests of bees, but I omitted to ask them for their evidence. Middleton (**1**) found bee larvae in the stomach of a badger near Oxford. Mr Owen Griffiths, keeper, Llanefydd, watched a badger raiding a nest at dawn. Three ravaged nests were found by the writer with badger hairs lodged in the heap of loose earth thrown out. These nests were near set 15. Raided nests were also found near sets 5, 7, 8, 14, 15, and at Pen y Cefn, but no badger hairs could be seen. In three cases, the raided nests were about 9 in. deep in clay soil, and it would have taken a powerful digger to get at them.

The badger is stated by many gamekeepers to raid wasps' nests. A piece of paper comb from a wasps' nest was found a yard or so from a grass litter that smelt strongly of badger, in a clearing between blackthorns and brambles a few yards from the deserted set E. A raided nest found at Tywysog was within a yard of one of the holes of set A. The largest exposed nest was about 10 yd. from set 11. No badger hairs could be seen about any raided wasps' nests: but, with the wasps still in residence, the writer did not wait to search for any.

The badger is regarded by most gamekeepers as a danger to pheasants' eggs. There is *prima facie* evidence in the egg shells seen by Mr Walter Jones,

of Garn, in the stomach of a badger, but that evidence depends for its value on Mr Jones's accuracy of identification. Fragments of a lapwing's and a pheasant's egg shells were apparently unaffected in colour and shape after 24 hours' soaking in 30 c.c. of 0·2 % hydrochloric acid plus about 1 c.c. of pepsin extract at 30–40° C., which seems to indicate that they would be easily recognisable in the stomach after subjection to the influence of the gastric juice. Mr Andrews, of Eriviatt, has seen badgers' padmarks by raided pheasants' nests usually at the time of hatching. On the other hand, Mr Telford, of Clawdd Newydd, who was a gamekeeper on Lord Carlisle's estate in Yorkshire, where badgers were protected, says that there were 15 pheasants' nests in a wood near sets containing 30 or 40 badgers, and the eggs were not touched until they were ready to hatch, when a fox took them all. The writer omitted to ask him how he knew it was a fox, but Mr Andrews has often seen foxes' footprints by raided pheasants' nests. No pheasant was harmed.

Considering the number of sets near Denbigh and the number of farms keeping poultry, badger raids on hens seem to be rare. Only three instances have been found. Mr Jackson, keeper, Galltfaenan, said that he had put four hens under coops in a fenced-in spinney. The four coops were overturned by some animal, and the hens carried off. Soon after, Mr Jackson found a hen dying inside a coop, in a wired and netted hen run, with a torn throat and exposed windpipe; on one wall of the coop which was shown to me were marks similar to those I had seen on the bark of a tree 15 ft. from set 12. The next evening and following morning, Mr Jackson waited in the paddock and shot a badger inside it. Afterwards, no more hens were taken. Mr David Jones, keeper, Gellifor, described a similar case: a Llanbedr farmer had had many hens killed in the henhouse. He watched at night and shot a badger outside the henhouse. He lost no more hens. Mr Roger Williams, Llansannan, also lost no more hens after shooting a badger weighing 42 lb. Charles Thomas, of Wrexham, states that he sat up near a hencoop which had been raided, to watch for the marauder, and his farmer companion 30 yd. away shot a badger by the hencoop. On the nights of the raids some animal had scraped a hole under the wooden wall of the hencoop into the interior. Mr Walter Jones describes how three badgers were found, and one shot, inside a hencoop in which they had disembowelled 60 out of the 160 pullets, after having forced a hole through the wire netting of the hen run and driven a shaft from outside through the floor of the coop. He also states how a farmer shot a badger in a turkey coop; no turkeys had been killed, but, since the coop was a lean-to shed against a bank of earth, the badger had climbed onto the bank and had forced its way through the rotten timbers into the shed. On the other hand, Mr Telford said that he had kept hens under coops in a field near the badger sets on Lord Carlisle's estate, but not a hen was touched. Mr Edwards, of Gwaenynog, has found game bones and rabbit bones in a set, and Mr Telford said that when the badger scoops out his old winter bedding, sometimes a lot

of bones come out with it. Mr Roger Williams has found a dead lamb in a badger set, but it is possible that a fox dragged the lamb into the set, or that the lamb was dead when the badger found it. One yard away from the grass litter described with regard to wasps' nests was part of the skin of a mole. This is of interest, since J. E. Harting (2) cites a case where a partly devoured mole was found in a nest of young badgers.

4. HABITS

Mr Walter Jones knew a man who had tracked badger spoor across the snow. Mr Roger Williams says that badger padmarks have been seen in the snow on the Hiraethog moors, which are near the 1000 ft. line. Mr Gardener Roberts, of Elwy Bank, Trefnant, has seen badger padmarks in the snow by the River Elwy. I saw fresh padmarks near the end of December in mud in two places, three-quarters of a mile apart; one was by set 14. At the same period I saw padmarks by sets 3, 4, 11 and N, while sticks were pushed aside from sets 8, 13 and 14. Mr David Jones, keeper, Gellifor, described the badger's winter sleeping chamber as being enclosed by bracken fronds and lined with dry powdery bracken and grass, whilst in the mouth of the set may be a plug of grass, which, he said, distinguished a badger's set from a fox's den: this is the only indication of hibernation which has been obtained.

An observation that I have not seen described is that the badger's dung is usually laid in holes scraped out of the ground, and is found together with other dung. This was seen by sets 3, 8, 11, 13, 14, 15 and G.

The badger's bed of dried grass referred to above was on the south edge of a wood and was concealed by dense thorn bushes and brambles, under which were two or three runs. It may have been used for sleeping or for basking in the warmth of the sun, though no sun could reach it in the early morning. The evidence that it was a badger's litter was the strong, almost unmistakable, smell of badger in the grass.

Five gamekeepers agree that the badger is difficult to trap with the ordinary spring trap. Three keepers, Mr Andrews, Mr David Jones, Gellifor, and Mr Williams, Llywesog, have found black badger hairs in sprung traps. Mr Andrews had set a trap four times in the mouth of a set, found it sprung the first time, then put stakes on both sides to force the badger on the trap, but found it sprung again. Next time he barred the front of the trap with another stake, but it was sprung again. The fourth time he set a stake across on the set side, fencing the trap clean round, but it was sprung again. Each time the trap was sprung there were a few black hairs in the jaws. So far it has not been possible to discover how a badger can spring a trap without getting caught.

Four gamekeepers said that in digging out a badger they cannot dig after it as quickly as it burrows away from them where the soil is sandy. It stops

the passage with fresh soil excavated as it goes ahead. In clay soil the badger can usually be overtaken.

5. Reputed damage done by badgers

There is little room for doubt about trampling down corn. The evidence of oats and wheat husks in the stomach points strongly towards it. Mr Parry, farmer, of Rossa Bach, blames badgers for trampling his corn, and Mr Roger Williams knew of badger runs leading into the standing corn. But some of this damage attributed to badgers may be due to other causes; the writer has seen a sow wander into a field of ripening corn, and also about 50 sq. yd. of corn flattened out in a field half a mile from set 7.

Damage to pheasants' eggs seems to be the chief reason for killing badgers on estates where game is preserved. In one instance a badger was killed on account of its bad name alone. There is no reliable evidence for the claim that badgers kill lambs.

Since rabbits are regarded as a pest around Denbigh, the badger, in digging out their young, seems to be useful to the farmer, but against this is the damage done in trampling and eating corn.

6. Summary

1. In August 1935 there were 20 occupied badger sets in the neighbourhood of Denbigh (48–50 sq. miles).

2. In this agricultural area the sets were mostly restricted to wooded hillsides, usually of clay soil, often in a river valley. Most of them were far from farms, but distribution was apparently limited by the above conditions, and within the limits of the area surveyed, altitude seemed of little consequence. Persecution by gamekeepers and farmers seems to be a limiting factor.

3. Dung examinations showed that the badgers studied eat rabbits (*Oryctolagus cuniculus*), dorbeetles (*Geotrupes stercorarius*), wheat, oats and acorns. Other observations indicate that nests of bees and wasps are raided, and pheasant eggs, poultry and earthworms eaten.

7. Acknowledgments

I would like to thank Mr Charles Elton, Mr Middleton, Mr Dell, my tutor, and my father for correcting and criticising my paper. I am grateful for help from Miss Frances Pitt, the gamekeepers and others, especially from Mr Andrews of Eriviat.

References

1. Middleton, A. D. (1935). "The food of a badger (*Meles meles*)." J. Anim. Ecol. 4: 291.
2. Harting, J. E. (1872). The Field, March 23, 1872.

THE FOOD OF CADDIS FLY (TRICHOPTERA) LARVAE

By H. D. SLACK

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(*With 2 Figures in the Text*)

1. Introduction

Throughout the literature relating to the life histories of the Caddis Flies (Trichoptera), there are references to the larval food. Such references are either of a general nature, or must be taken to refer to the habitat of the particular larvae described by the author. These notes are intended to be accepted in the latter sense. They refer to some of the Trichoptera found in a limited area—part of the upper reaches of the River Test, a river of the type known as a "chalk stream", flowing through the chalk of northern Hampshire. In its upper reaches it is a shallow river, the depth rarely exceeding 2 ft., except where the water level is raised for the purpose of working water mills, three of which occur in the area. The bed, of flint stones and gravel with a deposit of silt wherever the rate of flow permits, supports an abundant flora.

Without attempting to give an exhaustive account, the principal elements of the flora may be mentioned. *Ranunculus fluitans* (Lam.), *Apium nodiflorum* (Reichb.), *Potamogeton densus* (L.), *Callitriche aquatica* (Sm.), *Hippuris vulgaris* (L.), *Sparganium erectum* (L.) and *S. minimum* (Fries) are phanerogams which all attain dominance in various regions; the first three in the shallow regions, the remaining species in the mill-heads where the water is deeper and the bed covered with a deposit of silt. The moss, *Fontinalis antepyretica*, is frequent on stones and the wooden supports of bridges.

Among the principal genera of filamentous Algae may be mentioned *Ulothrix*, *Vaucheria*, *Spirogyra* and *Cladophora*. The Diatom flora is particularly rich, both in species and numbers; those of outstanding importance being *Melosira*, *Cocconeis*, *Synedra*, *Fragillaria*, *Nitzschia*, *Gomphonema* and *Navicula*.

An abundant fauna naturally occurs with such a flora. The chief elements capable of playing a part in the food relations of the Trichoptera larvae are—Crustacea: Cladocera and Copepoda, *Gammarus* and *Asellus*; Mayflies (Ephemeroptera): *Baëtis*, *Centroptilum* and *Ephemerella* nymphs; Neuroptera: *Sialis* larvae; Trichoptera larvae; Diptera: *Simulium* and Chironomid larvae; Mollusca: *Bithynia*, *Valvata*, *Physa*, *Limnaea* and *Planorbis*. As regards distribution: Cladocera, Copepoda, *Asellus*, *Sialis*, some Trichoptera and all the

Mollusca except *Physa* attain their greatest population density in the silted regions.

2. Material and methods

Twelve types of larvae were examined belonging to seven families:

Limnophilidae:
Glyphotaelius sp.
Limnophilus rhombicus (L.)
Anabolia nervosa (Leach) Curt.
Stenophylax sp.
Halesus sp. (spp.?)
Sericostomatidae:
Sericostoma personatum Spence
Silo nigricornis Pict.
Odontoceridae:
Odontocerum albicorne Scop.
Leptoceridae:
Leptocerus sp.
Molannidae:
Molanna angustata Curt.
Hydropsychidae:
Hydropsyche sp.
Rhyacophilidae:
Rhyacophila dorsalis Curt.

Owing to the difficulty which exists in identifying the species of larval Trichoptera, no attempt was made to carry the determination of some of the types beyond the genus.

Some difference exists between the periods at which the larvae were collected, so that a uniformity of flora and fauna available as food cannot be assumed for all the genera recorded. All the larvae were examined at advanced stages of development and were collected during the months of April, May and June. In this period changes would occur in the aquatic life of the river. An investigation of the numerical variations of the fauna and flora showed that the population density of Diatoms and Chironomid larvae decreased, while that of other Algae other than Diatoms, and of Ephemeroptera nymphs increased; but it also showed that these organisms were present throughout the period in numbers sufficient to render them readily available as food.

In the case of *Odontocerum*, *Hydropsyche*, *Glyphotaelius*, *Limnophilus*, *Anabolia*, *Stenophylax* and *Halesus*, the material represents two or more generations. In these the records give a more faithful representation of the general food than is the case with the remaining genera, which were each collected at one particular time.

The larvae were dissected immediately after being killed, the alimentary canal was removed to a glass slide and the contents expressed for examination under the microscope.

3. Results of examination

With the exception of the Diatoms, most of the food organisms were in a fragmentary condition, but sufficient structural details generally remained to enable them to be determined. Table 1 records the food found in the gut contents, and the numbers of individuals in which each type of food organism occurred.

Table 1. *Numbers of larvae containing different food materials*

	Glypho-taelius sp.	*Limnophilus rhombicus*	*Anabolia nervosa*	*Steno-phylax* sp.	*Halesus* sp. (spp.?)	*Sericostoma personatum*	*Silo nigricornis*	*Odontocerum albicorne*	*Leptocerus* sp.	*Molanna angustata*	*Hydropsyche* sp.	*Rhyacophila dorsalis*
No. of larvae examined ...	10	10	18	10	20	10	10	12	5	12	10	9
No food	.	.	.	.	.	.	.	2	.	.	.	2
PLANTS												
ALGAE												
Isokontae												
Ulothrix	4	.	.	3	.	3	.	1	2	..	4	.
Cladophora	.	.	.	1	1	.	.	.	.	.	.	.
Chaetophora	.	.	.	2	.	.	.	1	.	.	.	.
Other Isokontae	.	.	7	.	6	.	.	1	.	.	.	.
Conjugatae												
Closterium	.	.	2	.	.	.	.	.	.	.	2	.
Siphonales												
Vaucheria	.	.	2	5	2	.	.	.	.	.	.	.
Diatomales												
Centricae	9	1	16	5	12	8	6	6	1	.	9	2
Pennatae		4		4		5	10	3	1	10	8	2
Rhodophyceae												
Batrachospermum	.	.	.	.	1	.	.	.	.	.	.	.
PHANEROGAMS and BRYOPHYTES												
Leaf fragments	9	10	4	8	7	7	1	.	1	.	.	1
ANIMALS												
ARTHROPODA												
Crustacea												
Cladocera	.	.	.	.	.	1	.	1		5	.	.
Copepoda	1	.	1	.	.	.	.	.	.		3	.
INSECTA												
Baëtis spp. nymphs	.	.	7	.	.	.	.	2	.	.	1	.
Trichopteran imagines	.	.	.	.	1	1	.	.	.	.	.	.
Trichopteran larvae	1	.	.	.	1	.	.	5	.	.	.	5
Simulium sp. larvae	.	.	.	.	.	.	.	.	.	.	.	1
Chironomid larvae	.	.	1	.	.	.	.	.	1	.	3	1
Other Insecta	.	.	.	.	.	1	.	2	.	3	.	.
ARACHNIDA												
Acarina	.	.	.	.	.	.	.	.	1	.	.	.
MOLLUSCA												
Limnaea sp.	.	.	.	.	.	.	.	.	.	2	.	.
Mineral and organic debris	1	7	.	7	17	9	10	8	3	12	6	7

Glyphotaelius sp.

The larvae of this species were the only material not collected from the river itself. They were obtained from a channel whose grass-covered bed had been recently filled by admission of water from the river. The grass was covered by an abundant growth of Algae (Diatoms and Isokontae) which supported a rich fauna, principally of Ephemeroptera nymphs, Cladocera, Copepoda, *Gammarus* and Trichoptera larvae. Fragments of grass leaves, together with their epiphytic Diatoms, formed the bulk of the gut contents, and animal food was only represented by single occurrences of Copepods and a Trichopteran larva.

Limnophilus rhombicus L.

A typical habitat of *L. rhombicus* is a region where the water is relatively deep and of a low rate of flow; and where there is a profusion of phanerogams and *Fontinalis*. The food comprised fragments of *Ranunculus fluitans*, *Hippuris vulgaris*, *Sparganium* spp. and *Fontinalis* sp., including both dead and living material. Diatoms epiphytic on these plants, such as *Cocconeis* spp. and *Melosira varians* (Ag.), also occurred and would have been taken in with the leaf fragments.

Anabolia nervosa (Leach) Curt.

This species has a wide range, being found on exposed silt, stones and vegetation. While primarily phytophagous, the gut contents showed that it would also take living animals. In an aquarium *A. nervosa* were seen to seize and devour *Baëtis* nymphs with a facility not to be expected from an animal so slow in its movements and encumbered by the unwieldy case characteristic of the species.

Carpenter (1) considers *Anabolia* to be a detritus feeder, on the "larger particles of decaying matter", but the larvae examined contained living plant material which varied with the type of habitat. Larvae from the silt yielded Diatoms, *Closterium* and *Vaucheria*: those from *Ranunculus* yielded epiphytic Diatoms, filamentous Algae (e.g. *Vaucheria*) and leaf fragments, *Baëtis* nymphs and Chironomid larvae.

Stenophylax sp.

The species was probably *S. stellatus* Curt., of which the imago is very numerous and the only species that has been observed. The larva has a similar range to that of *Anabolia*, but the food more closely resembled that of *Limnophilus rhombicus*, except that filamentous Algae formed a large proportion. The gut contents in some cases consisted principally of *Vaucheria*, *Ulothrix* and *Chaetophora*. The Diatoms observed were epiphytic forms, especially *Melosira*.

Halesus sp. (or spp.?)

The *Halesus* material may have consisted of more than one species, as no attempt was made to carry identification beyond the genus. *H. digitatus* Schr. and *H. radiatus* Curt. are the species which have been identified in the imaginal state. From the gut contents *Halesus* would be judged to be chiefly phytophagous, twenty individuals yielding only two instances of animal food. Felber (2) states that *H. tesselatus* Rambur. is particularly carnivorous, and gives an instance where fifteen larvae attacked and devoured a living *Triton alpestris*. *Halesus* larvae, of the same species as those used for gut content examination, in an aquarium, were found to bear out Felber's observations. One larva seized a living trout alevin, killed and ate it; while, on another

occasion, several larvae devoured a Syrphid fly which was floating on the water surface.

Sericostoma personatum Spence

The gut contents resembled those of *Halesus* with the additional record of a Cladoceran, but the leaf fragments were nearly all of dead leaves (both living and dead occurring in *Halesus*). *Sericostoma personatum* generally occurs in regions of stones and gravel and would find there a quantity of dead plant material from the surrounding vegetation. For *S. personatum* from Lake Windermere, Moon (5) records "algal felt and *Littorella* fragments", presumably from living plants.

Silo nigricornis Pict.

This is another species frequenting regions where *Sericostoma* is generally to be found, but it does not resemble the latter in feeding habits. The gut contents suggest that it is entirely phytophagous and a typical Diatom feeder. In all but one case the food consisted of Diatoms of the species found on the river bed; the single exception containing a few leaf fragments. As the material was collected from different stations, it is unlikely that the uniformity of the gut contents, as regards the absence of food other than Diatoms, was due to the absence of such food from the regions where the larvae were found.

Odontocerum albicorne Scop.

The habitat is again the regions of stones and gravel, but generally where the stones do not exceed 1 in. in diameter. Both plant and animal organisms occurred, as shown in Table 1, the former being mainly Diatoms. Debris of phanerogams, found by Silfvenius (cited in 6, p. 596) to feature importantly in the food of *Odontocerum*, did not appear in this material. The presence of Trichoptera larvae in five individuals suggests that it preys on other members of the order. These ingested larvae were in a fragmentary condition preventing their exact determination, but structural characters remained which indicated that they were all Polycentropidae.

Leptocerus sp.

The five specimens were collected from different stations, and the results indicate a wide range of food, in accordance with the regimen of the family given by Rousseau (6, p. 601). The occurrence of a non-aquatic Acarine suggests that dead as well as living animals may be accepted as food.

Molanna angustata Curt.

Occurring exclusively on the silt, *Molanna* was found to obtain its plant food entirely from the silt Diatoms, a mass of such types as *Cymatopleura*, *Navicula*, *Stauroneis* and *Nitzschia* being present in nearly all the larvae. The type of habitat favours the Entomostraca, and it is not surprising to find

them represented in the gut contents of a genus considered to be mainly carnivorous (**6**, p. 665), although in this instance principally vegetarian. The particular area from which the material was collected abounded in *Limnaea stagnalis* L. and *L. pereger* Müll., for it was an enclosure used for rearing them. Therefore the fragments of mollusc shell recorded would probably belong to these species, particularly as a propensity for feeding on *Limnaea* was confirmed experimentally in the aquarium.

Hydropsyche sp.

The gut contents consisted of small organisms of an order of size consistent with the method of obtaining food adopted by *Hydropsyche*, i.e. by means of a net collecting minute organisms and debris particles carried to it by the flow of the stream (**1**). Hydropsychidae have been stated to be entirely carnivorous (**4**) and again to be omnivorous (**7**); Silfvenius (cited in **6**, pp. 540–1) noted a case from Finland where *Hydropsyche* larvae had hollowed cavities in the wood of a bridge. In this material Diatoms proved to be dominant and, where animal food was present, not more than two specimens occurred in each individual.

Rhyacophila dorsalis Curt.

R. dorsalis was the predominantly carnivorous species of those examined. Two specimens contained Diatoms: one Diatoms alone; the other Diatoms, a fragment of *Fontinalis* leaf and a Trichopteran larva, the last apparently being a Polycentropid. In the remaining cases where food was present, Trichopteran larvae were found, with the addition in two specimens of a *Simulium* larva and a Chironomid larva.

4. Discussion

An attempt to classify these records into phytophagous, omnivorous and carnivorous groups, shows that none of the types was entirely carnivorous and only three purely phytophagous. This is shown by Table 2.

Table 2. *Numbers of larvae containing different classes of food*

	Type of food			
	Plant	Animal	Plant and animal	No. of larvae examined
Glyphotaelius sp.	9	0	1	10
Limnophilus rhombicus	10	0	0	10
Anabolia nervosa	11	1	6	18
Stenophylax sp.	10	0	0	10
Halesus sp. (spp.?)	18	1	1	20
Sericostoma personatum	7	0	3	10
Silo nigricornis	10	0	0	10
Odontocerum albicorne	2	1	7	12
Leptocerus sp.	2	0	2	5
Molanna angustata	3	1	7	12
Hydropsyche sp.	4	1	5	10
Rhyacophila dorsalis	1	5	1	9

The statement that none of the types was exclusively carnivorous owes its validity to the fact that one specimen of *Rhyacophila* contained plant food alone and one plant and animal food. No plant food was found in any of the remaining specimens of this species, from which it would be inferred that the diet is normally carnivorous. The remaining species, found to be omnivorous, apparently rely primarily on Phanerogams, Bryophytes or Algae, but would also devour any animals with which they came into contact, if these were sufficiently small and defenceless.

Various suggestions have been put forward correlating the feeding habits with morphological characters, either directly, or indirectly through the systematic classification. Considering the latter first, Martynov (3) states that Annulipalpia (Martynov) are "mainly carnivorous" and Integripalpia (Martynov) are "phytophagous by preference". Of the former suborder, Rhyacophilidae and Hydropsychidae are represented in these notes, and of the latter, Odontoceridae, Molannidae, Leptoceridae, Limnophilidae and Sericostomatidae. The occurrence of only two families of Annulipalpia renders it difficult to determine how far Martynov's generalisation can be applied. It is certainly true of Rhyacophilidae but doubtful in the case of Hydropsychidae. That Integripalpia are preferentially phytophagous seems, on the whole, to be a correct conclusion for the material here discussed.

Two structural characters which have been used are the presence or absence of "brushes" of setae on the mandibles and the position of the eyes (6, p. 372). Silfvenius advances the theory that larvae having brushes on both mandibles are primarily phytophagous, those possessing one on the left mandible only are omnivorous, and those without brushes carnivorous. Applying this grouping to the larval types examined, *Glyphotaelius*, *Anabolia*, *Stenophylax*, *Halesus*, *Sericostoma* and *Silo* fall into the first group, *Hydropsyche* into the second, and *Limnophilus rhombicus*, *Leptocerus*, *Odontocerum*, *Molanna* and *Rhyacophila* into the third (Fig. 1). Two of the six types in the nominally phytophagous group proved to be purely phytophagous, namely *Silo* and *Stenophylax*. The second, the omnivorous group, claims only one type, *Hydropsyche*, which qualifies for inclusion in the group. The third group certainly includes the more generally carnivorous types, *Rhyacophila* and *Molanna*, but all its members were omnivorous to some extent, except *Limnophilus rhombicus*, an entirely vegetarian species. It is noticeable that *L. rhombicus* is a type which fed on fragments torn from the leaves of macrophytes, whereas the species possessing mandibular brushes were those in which more delicate fare, such as Diatoms, ranked largely in the gut contents: the probable function of the brushes being to carry small organisms into the mouth.

The form of the mandibles also serves as an approximate guide. *Silo nigricornis* possesses stout mandibles with a large molar surface, without teeth, and is a typical Diatom feeder; while *Rhyacophila* has long sharply pointed

Fig. 1. Mandibles of Trichoptera larvae (left mandible, posterior view). A. Types with brushes of setae on both mandibles: 1, *Glyphotaelius* sp. (×33); 3, *Anabolia nervosa* (×33); 4, *Stenophylax* sp. (×22); 5, *Halesus* sp. (×50); 6, *Sericostoma personatum* (×33); 7, *Silo nigricornis* (×50). B. Types with a brush on left mandible only: 11, *Hydropsyche* sp. (×33). C. Types without brushes: 2, *Limnophilus rhombicus* (×22); 8, *Odontocerum albicorne* (×33); 9, *Leptocerus* sp. (×82); 10, *Molanna angustata* (×33); 12, *Rhyacophila dorsalis* (×44).

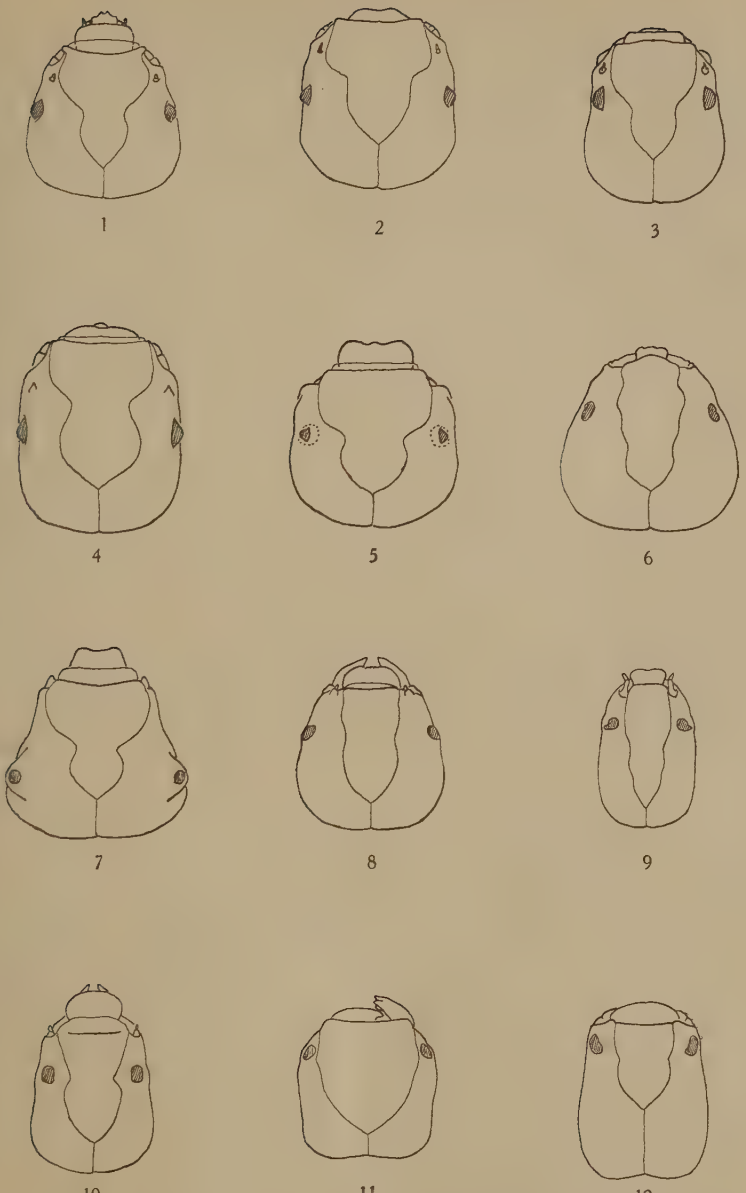

Fig. 2. Position of the eyes in Trichoptera larvae. 1, *Glyphotaelius* sp.; 2, *Limnophilus rhombicus*; 3, *Anabolia nervosa*; 4, *Stenophylax* sp.; 5, *Halesus* sp.; 6, *Sericostoma personatum*; 7, *Silo nigricornis*; 8, *Odontocerum albicorne*; 9, *Leptocerus* sp.; 10, *Molanna angustata*; 11, *Hydropsyche* sp.; 12, *Rhyacophila dorsalis*.

biting faces. The omnivorous forms and those whose food requires tearing or cutting generally show a development of from three to five denticles.

The correlation of the position of the eyes, pointed out by Wesenburg-Lund (7), in which an anterior position is held to denote a carnivorous and a posterior position a phytophagous regimen, is well shown also by *Rhyacophila* and *Silo*, respectively (Fig. 2). But from the material examined, *Limnophilus rhombicus* and *Stenophylax* would be judged to be as purely phytophagous as *Silo*, yet the almost medially placed eyes give no clue to the fact the eyes of several omnivorous forms being similarly disposed. There seems to be a similar situation as regards the ratio of the width of the head to the frontal length. In the more carnivorous types this ratio equals or exceeds 1 : 1·5, while in the more usually phytophagous forms it does not exceed 1 : 1·3. But here again, no hard and fast rule emerges, for *Hydropsyche* has a ratio of 1 : 1.

So far as the larval types referred to in these notes are concerned, these morphological characteristics can only be said to give a wide approximation of the feeding habits. They are more truly indicative in extreme cases; for example, in the eye positions in *Rhyacophila* and *Silo*. The occurrence of mandibular brushes would seem to denote the quality of the food material rather than its identity.

5. Acknowledgments

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6. Summary

1. The Trichoptera larvae, whose food is described, were collected from an area on the River Test, Hampshire, of which a brief account of the flora and fauna is given, with respect to the food relations of Trichoptera.

2. The results of examination of the gut contents of 136 larvae are reported. These belonged to 12 types, viz. *Glyphotaelius* sp., *Limnophilus rhombicus* L., *Anabolia nervosa* (Leach) Curt., *Stenophylax* sp., *Halesus* sp., *Sericostoma personatum* Spence, *Silo nigrocornis* Pict., *Odontocerum albicorne* Scop., *Leptocerus* sp., *Molanna angustata* Curt., *Hydropsyche* sp., *Rhyacophila dorsalis* Curt. A description is given of the food material found in each type.

3. Most of the types were found to be primarily phytophagous, but only three entirely so: these three being *Limnophilus rhombicus*, *Stenophylax* sp. and *Silo nigricornis*. The remaining forms were omnivorous to varying degrees, *Rhyacophila dorsalis* being the predominantly carnivorous.

4. Suggestions correlating morphological characters with feeding habits are discussed, with the conclusion that such correlations can only be applied approximately within wide limits.

REFERENCES

1. **Carpenter, K. E. (1928).** "Life in inland waters," 41–2. London.
2. **Felber, J. (1908).** "Die Trichopteren von Basel und Umgebung mit Berücksichtigung der Trichoptera-fauna der Schweiz." Arch. Naturgesch. 74: 199.
3. **Martynov, A. B. (1930).** "On the Trichopterous fauna of China and Eastern Tibet." Proc. Zool. Soc. Lond. 65.
4. **Miall, L. C. (1895).** "The natural history of aquatic insects," p. 242. London.
5. **Moon, H. P. (1934).** "An investigation of the littoral region of Lake Windermere." J. Anim. Ecol. 3: 8.
6. **Rousseau, E. (1921).** "Les larves et nymphes aquatiques des insectes d'Europe (morphologie, biologie, systématique)," vol. 1. Brussels.
7. **Wesenburg-Lund, C. (1913).** "Wohnungen und Gehäusebau der Süsswasserinsekten." Fortschr. Naturw. Forsch. 9: 107.

THE HABITATS OF FRESH-WATER MOLLUSCA IN BRITAIN[1]

By A. E. BOYCOTT

Ask now the beasts, and they shall teach thee. Job xii. 7

(*With* 63 *Figures in the Text*)

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1. Introduction

We have 62 fresh-water species, 26 bivalves and 36 gastropods, 10 of which are operculates and breathe by gills while the rest are pulmonates which normally breathe air. There are also 4 operculates (*Assiminea grayana*, *Paludestrina stagnalis* (*ulvae*), *P. ventrosa*, *Amnicola confusa*) and 2 pulmonates (*Ovatella bidentata*, *Phytia myosotis*) which affect the junction between fresh and salt water, but I know little about their habitats and shall not consider them further.

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Fresh-water differ from terrestrial habitats in two important particulars. (*a*) The environment is much more uniform from place to place than on land and less variable in any one place from time to time. Hence there is less difference between the inhabitants of various loci: no two watery habitats which are at all favourable to Mollusca will have such diverse contents as, for example, an old acid woodland and a chalk down. It follows too that transplantations, natural or deliberate, should be more likely to succeed than with land Mollusca, and that experimentation under controlled conditions is relatively easy, though it needs far more exploration than it has received from those who like keeping aquaria. (*b*) The habitats are mostly divided into discrete units and are definitely limited in size: some of them are presumably infinitely large from the molluscs' point of view, but others are so small and circumscribed that it seems likely that questions of roominess must arise, almost or quite unknown on land.

For descriptive purposes we may distinguish several groups of habitats classified by common human usage, though these do not of course necessarily correspond with the essential categories of molluscan ecology: they naturally grade into one another and it would be waste of time to try to define them too closely:

Rivers.

Streams.

Springs and the streamlets and trickles which come from them.

Canals.

Ditches.

Lakes, i.e. bodies of water large enough for the wind to raise significant waves and generally too deep in the middle parts for phanerogamic vegetation.

Ponds, of $\frac{1}{2}$ acre downwards and mostly of the order of 400 sq. yd. ($\frac{1}{12}$ acre) or less.

Marshes.

Ponds and, less often, lakes and marshes have to be further distinguished into (1) those through which a stream of water runs either perennially or in the winter and which are thus in communication with the river systems ("running"), and (2) those without any direct connection with another watery habitat ("closed"). We also have to note whether any of the smaller habitats always contain water or whether they dry up in the average summer ("drying") or in exceptional droughts. Ditches include permanent draining ditches connected with marshes, often of considerable size, and ditches made to keep land dry in wet weather which contain no water for most of the year.

The nomenclature is confused in a variety of ways. Thus what would be called a pond in lowland country may be dignified as a tarn, loch, lough or llyn in the hills. A "lake" in many parts of England may be a stream; a "pool" may be a pond, a good-sized lake or a slow-flowing piece of a river; a "ditch" in Ireland sometimes means a fence or bank

(259), and you may either fall into a "dyke" or climb over it; "spring" may mean a wood, and the dialect dictionary would no doubt reveal many other possibilities of perplexity, most of which would, as I hope to show, be solved by a knowledge of the Mollusca present.

It is evident that man has had a good deal to do with many of these habitats, and his influence on our water Mollusca is perhaps hardly less than on the land species. Canals, ditches, marl pits and brick diggings are entirely human and so are most ponds: they provide habitats of which there are few or no natural replicas. Man's interest has always been to get rid of marshes, drain river valleys and generally to make as clear a distinction as he can between dry land and water. In the result most of the places in which we collect, especially in the southern two-thirds of England, are more or less unnatural.

2. General biology

(*a*) *Food*

The bivalves feed at random by sucking in water and entangling any particles it may contain in their intestinal mucus "with catholic impartiality" (256), though Allen (192) thinks that the labial palps can exercise a certain amount of discrimination. They are therefore dependent on the Algae, etc., which happen to be present, which they filter out quickly and very efficiently, as Dodgson (20) has shown in his work on the cleansing of *Mytilus* from bacterial contamination. Allen found that a 200-gm. *Lampsilus* passed through 35 litres (10 gallons) a day; Dodgson got 53 litres (15 gallons) for *Mytilus* 3 in. long. Algologists would find the intestines of mussels worth study: Latter (1, p. 174) gives a list of the things found in *Anodonta*, and Prof. E. J. Salisbury got some rare Algae in some we caught in the Elstree reservoir. Except *Dreissena*, the bivalves live mostly on the bottom, though *Sphaerium corneum*, *S. lacustre* and some *Pisidium* often climb up plants, and sand or mud in some form seems to be a necessity: *Sphaerium* and *Pisidium* do no good in aquaria without it. But whether this substratum is needed to grow their microscopic food or to give them something to burrow in, I do not know: it may be useful in both ways.

The gastropods are more mobile, can fix themselves anywhere with their adhesive feet, and have the same type of rasping apparatus as the land Mollusca, so that selection is possible. They feed on the decayed remains of water plants and especially on Algae which they scrape off the leaves of the plants, the mud, stones and other surfaces (e.g. floating logs), as may be well seen as they crawl over the glass of an aquarium. In some loci (e.g. mountain lakes, or cement tanks), where there is little or no obvious vegetation it seems quite clear that the normal food of the *Limnaea peregra* and *Ancylus fluviatilis*, which may be abundant, is the algal slime on the stones. As with land Mollusca, it is most exceptional to see any evidence in the field that they eat

the green leaves of the higher plants among and on which they live: I have seen it only once when an exceptional crowd of *Limnaea stagnalis* had eaten a bed of *Helosciadium* to pieces. Nor do they commonly do so in captivity, even when their rate of growth is seriously diminished by overcrowding and one may reasonably suppose that they are short of food. On the other hand, as slugs and snails do, they will eat cultivated plants such as cabbage and lettuce, though more readily when they are partly decayed. Warrington's (**2**) record that *Limnaea stagnalis* eats *Valisneria* greedily in aquaria I regard as exceptional rather than regular, also R. Welch's (**3**) note of "rare water-lily leaves" being destroyed by the same species and *Planorbis corneus*. At times they may be carnivorous and will eat meat, dead fish, etc.: as curiosities we may note that *Pl. corneus* has been caught eating the egg capsules of *Pl. vortex* (Sherborn (**4**)) and live *Limnaea peregra* (Cockerell (**5**)), and Webster (**237**) says it does best in aquaria with meat. They show the same liking as land snails for newsprint (**173**), cardboard, etc., and what they eat depends no doubt on what is available and on how hungry they are.

Limnaea peregra from any place where there is fine gritty silt will have some, often a great deal, in their stomachs; *Ancylus fluviatilis* is the same (**261**). Aquarium experience shows that *Limnaea* get on quite well without this mechanical aid to digestion, though Colton (**207**) found that *L. columella* grew better if silt was provided. The operculate *Goniobasis* gets rid of its sand in captivity in about 14 days (**208**).

The well-known experiments of Semper showing a direct relationship between the volume of water in an aquarium and the rate of growth of *Limnaea stagnalis* have been carefully worked over again with *L. peregra* by F. M. Turner (**6**), who concluded that the main if not the only factor was the food supply. He found, for example, that the rate of growth of snails brought up in standard jars was a function of their number, and that a single snail could be grown to its full adult size in 10 or 15 c.c. of water if it were fed well enough. The bad, and in the end fatal, effect of overcrowding young snails in aquaria is obvious enough, and it seems quite possible therefore that the abundance of a mollusc in a locus of limited size may depend on the food supply, though whether the occurrence of any species is so determined is problematical. Shortly before his death Turner had been feeding *L. peregra* on pure cultures of green Algae and had obtained some evidence of selective preferences, but *I know of no reasons for thinking that in nature any species of snail has any direct relation to any particular plant.* Snails like a good supply of green plants because these, while alive, oxygenate the water and provide surfaces for algal growth, but the specific associations which can easily be seen are, as with the land Mollusca, due to the plant and the snail both happening to flourish in the same kind of locus. In my study of the Aldenham ponds (**7**), for instance, I worked out several statistical specific concurrences between snails and plants (e.g. *Planorbis fontanus* with *Lemna trisulca*), but I do not suggest that there is any more intimate connection between them than there is between calcicole

land Mollusca and beech trees. Similarly, a good many Mollusca will generally be found (in England) with water-lilies or with *Potamogeton crispus*, because these plants usually grow in places which are on other grounds favourable for them, and incidentally the large flat lily leaves provide a convenient and profuse growth of Algae. But the snails can get on quite well without the plants and there is no essential biological connection between them.

(*b*) *Life histories*

Reproduction. The larger mussels (*Anodonta*, *Unio*) are generally described as unisexual and there is commonly a considerable excess of females: Bloomer (**10**), however, finds a good many hermaphrodites in *Anodonta cygnea*, and it seems pretty clear that individuals change their sex: each female produces about half a million glochidia. *Sphaerium* and *Pisidium* are hermaphrodite and evacuate well-grown young, naturally in small numbers. Crowther (**277**) finds usually 6 or 7 in *Sphaerium corneum* but up to 30: Thiel (**182**) has shown at Hamburg that it has two generations a year with free lives from October to August and August to October, producing about 10 young each time, so that the annual increase is about 100. *Paludina* (unisexual) is also viviparous with about 50 young, as is *Paludestrina jenkinsi* (parthenogenetic) with broods of 20 or 30. The other operculates lay eggs, but no one seems to know how many. The pulmonates are all hermaphrodite and lay eggs. *Limnaea peregra*, *L. auricularia*, *L. stagnalis*, *L. palustris* and some *Physa Planorbis* (**217**) and *Ancylus* are known to self-fertilise quite readily (**13**), and they can probably all do so if need arises though they prefer cross-fertilisation. How many eggs are laid in nature is not clearly known, and our information about what happens in aquaria is very imperfect: in some of the accounts (e.g. Rimmer (294)) there is complete confusion between the number of eggs laid and the number per capsule, though I suspect that the two figures are proportionate to one another since both depend on the size of the parent. In captivity some races of *Limnaea peregra* average about 500 and can achieve as many as 3000 (**11**); other smaller races produce 200 or so. Correspondingly Oldham's data (**12**) suggest about 1000 for *Planorbis corneus* while *Pl. nautileus* has about 30 young. Interesting details about egg laying are given for the Indian *Limnaea luteola* by Sechaiya (**215**) and for the American *L. columella* by Baily (**216**).

Length of life. The larger mussels develop slowly and live for many years: if the lines of growth represent annual increments, 10 or 15 years is a common age and 70 has been suggested. Hence destruction of the adults may seriously diminish the population, as has happened with *Unio margaritifer* in the Scotch pearl fishery (**14**) and in Ireland. *Sphaerium* and *Pisidium* appear to be annuals. *Paludina* lives for several years but probably not as long in nature as in captivity, where Oldham (**15**) has kept female *P. contecta* for 5 years and the males (which are smaller) for at least $3\frac{1}{2}$ years. Cleave and Lederer (**22**)

say of *P. contectoides* in America that the wild males live about a year and the females up to 3 years, and Annandale and Sewell (**147**) found the same for *P. bengalensis* in India: it has been known since Spallanzani that one impregnation will suffice for more than the current year. *Bithinia tentaculata* often has such well-defined growth marks and *Neritina fluviatilis* is sometimes so thick and encrusted ("gerontic") that it seems probable that they may live 2 or 3 years, but the rest of the operculates are presumptive annuals as *Paludestrina jenkinsi* certainly is. All the pulmonates are annuals with a natural duration of life of 9–15 months or less, except *Planorbis corneus*, which lives and goes on growing for 2 or 3 years and breeds correspondingly often (**12. 21**): Oldham has kept it in captivity up to 6 years. In hot summers *Limnaea peregra* may get through 2 generations in one season, as it may easily be induced to do in captivity (**11**, p. 57), and it has been found spawning in November in the underground water which comes out at Malham Cove at 46–48° F. all the year round (Percival MS.). Wild *L. truncatula* in Wales (**197**) normally have 2 or even 3 generations in a summer. This may explain why the largest specimens are found early in the spring and in Scotland. In America *L. columella* breeds a new generation about every 2 months in the laboratory (**23**).

I do not understand the statements that in central Europe (**16**, p. 39) and in north America (**17**, p. 51; **18**, vol. 1, p. 412) such species as *L. stagnalis* need 2 or even 3 years to reach maturity. It may possibly be true for places where a severe winter stops growth for several months, but it certainly does not apply to this country where the annual cycle can be clearly seen in wild *L. stagnalis*, *L. auricularia*, *L. peregra*, *Planorbis complanatus*, etc.

Parasitism, etc. In their early stages the large mussels are obligatory "parasites" on fish. Some American species can apparently pass through their metamorphosis in the parent's brood pouch (**214**), and for one the amphibian *Necturus* makes a good host: the claim (**213**) that they can be reared in simple nutrient solutions needs confirmation. In America, too, where a good deal of attention has been paid to mussels for the sake of pearl buttons, there is some (but not much) evidence that certain species have specific relationships with particular fish (**240**, summary and literature in **18**). In Britain, however, I know of nothing to suggest that fish can be dispensed with or that the kind of fish matters very much. Wilson (in **19**) notes the curious point that parasitic Copepods may so occupy the gills as to prevent the attachment of glochidia. No other fresh-water molluscs are dependent for development or in any other way on another animal.

It occurred to me at one time that the widespread discontinuous distribution of some uncommon species might be due to something queer in their life histories, possibly a parasitic phase. But I have bred the three most conspicuous instances—*Segmentina nitida* (from Lewes), *Amphipeplea glutinosa* (Co. Kildare) and *Limnaea glabra* (Leeds, Scotland) to maturity under conditions which excluded fairly satisfactorily the intervention of another animal or any special plant.

(c) *Mortality*

Enemies and parasites. Fresh-water Mollusca have many enemies. Domestic and domesticated ducks are the worst, and they can completely destroy all the Mollusca in a pond or ornamental water, though this drastic effect may be due as much to the putrefactive fouling of the water as to actual eating. I know of no instance where under natural conditions an enemy may be reasonably accused of exterminating any established species: the great majority of animals which prey on snails are more or less omnivorous, and when a snail population is reduced beyond a certain point they turn their attention to other foods which are easier to find: trout, for example, as Pentelow (**33**) and Slack (**34**) have shown, eat what they can get. Rats (**24**, **181**, **244**), water-shrews (**255**) and otters (**155**) eat mussels and snails. Herons and other birds no doubt kill a good many. Peacock (**222**) has occasionally found *Limnaea auricularia* and *Dreissena* on thrush stones, and Carter (**25**) has seen a thrush pick out *Limnaea stagnalis*, smash and eat it: I have watched a blackbird fish out *Planorbis corneus* from a tank in my garden several times, but no attempt was made to eat them. Bellamy (**26**, p. 246) says that in Devon crows pick mussels out of the rivers and drop them on rocks to smash them as gulls do cockles (**63**), and they have been seen eating *Anodonta cygnea* and *Unio pictorum* (**262**) and *Dreissena* (Oldham), which tufted duck will also dive for and then be robbed by gulls (**263**). Thompson (**264**) mentions a grey wagtail full of *Ancylus fluviatilis*. By general consent fish are very fond of snails which are highly esteemed as fish food in trout hatcheries and also for coarse fish: Hall (**27**) specially commends *Planorbis corneus*, *Limnaea peregra*, *L. stagnalis* and *L. auricularia*, and says that the newly hatched young "seem to be the most acceptable of any food to fresh-water fish". Fishing clubs in Yorkshire buy *L. peregra* in quantity for fish food (**30**), and various large species (including even *Dreissena* (**181**)) seem to be moved about a good deal to rivers and lakes where they do not rightly belong. But the interest of fish is not restricted to the fleshy sorts: several observers (**28**, **29**) have found large numbers of *Valvata piscinalis* in trout's stomachs which must be more shell than meat, as must *Paludestrina jenkinsi* (**253**); in the north of Scotland the contents of the trouts' stomachs are often made up almost entirely of *Pisidium* (Oldham), and Burnett discovered *Limnaea burnetti* because he had the curiosity to see what a trout from L. Skene had inside it. In aquaria Krull (**232**), Henson (**245**) and I have found leeches extremely destructive, and gastropods are said to be the natural food of *Glossosiphonia* and *Helobdella* (**31**, **253**), as they are of the rare bug *Aphelocheirus aestivalis* (**265**). Various carnivorous larvae such as *Hydrophilus* (**188**) and beetles such as *Dytiscus* eat eggs and young snails as may caddis worms (**12**); glowworm larvae readily eat *Limnaea* if they get the chance (**266**). The rotifer *Proales gigantea* is parasitic in the eggs of *Limnaea* (**267**). *Limnaea* frequently harbours the larvae of trematode worms,

often in immense numbers, and *L. truncatula* is well known as the usual intermediate host of the sheep fluke, but whether these parasites do the snails much harm seems doubtful unless they are present in great excess (**198**): *Valvata* and *Pisidium* may also be infected. In India and Portugal *Bilharzia* larvae definitely injure and kill their *Planorbis* hosts (**199**). Pelsencer (**268**) gives a long list of parasites. The common *Chaetogaster* is probably immaterial.

Mortality in the young. Whatever the precise destructive agents, field experience suggests strongly that those which are effective in keeping the snail populations within reasonable bounds act on the infants: the killing of adults is generally of no great moment and the eggs[1] seem to be fairly safe. One sees a pond, for instance, with vast numbers of capsules of *Limnaea peregra* or *Planorbis complanatus*, and on searching through them one finds that the eggs are developing in a healthy way almost without exception. Yet in two or three weeks' time it may be quite difficult to find the young snails, and it is exceptional to find young ones much more numerous than adults will be later on: the weeding out seems to occur very soon after birth, and the viviparous species are relatively immune. Similarly, if a reservoir goes dry and one can obtain a view of the mussels, the young ones do not seem to be more than enough to maintain the adult population. This infant susceptibility also applies to adverse physical and chemical conditions: eggs are resistant and can be moved about from one sort of water to another with impunity, and those of *Limnaea stagnalis* will develop normally either in distilled water or 5 % salt solution (**32**). But newly born snails have to be treated with a good deal of care, and they are easily killed by a sudden move to different water which older ones do not seem to notice. In nature, therefore, there is an immense "infant mortality". This does not occur if the changes and chances of wild life are excluded, for the whole of a brood of several hundred *L. peregra* may be safely reared in aquaria if they are given room and food enough. The intensity of selection obviously varies greatly in different species: a population of *Anodonta* would be maintained by the survival of less than 1 in a million of the young; *Limnaea peregra* needs perhaps 1 in 500, *Sphaerium* 1 in 10.

(*d*) *Dispersal*

It is possible for many water Mollusca to spread a long way by continuity of their habitats. A map dated 1870 included in the report of the Canal Commission (1909) shows 215 catchment basins in England and Wales: many of them are small coastal areas, but the Thames includes about 8 % of the whole, the Severn 7·5 %, and the Trent 7 %. The canals which were built between 1760 and 1810 joined together all the larger river systems, and the whole canal basin occupies about half of England and Wales (**8**, Fig. 63 and below, p. 173). Similarly in Ireland the Shannon drains 14 % of the country and in Scotland the Tay covers 8 %. *Planorbis acronicus* (**204**), recent and fossil, is found only

[1] In *Neritina* one embryo in each capsule of about 50 eggs eats the others before hatching.

in the Thames drainage: none of our other species is restricted to a single basin, nor does the natural arrangement of the rivers appear to exercise any decisive influence on their geographical distribution.

There are, however, a number of "closed"[1] habitats, i.e. restricted loci separated by land from any other water, and the occurrence of snails in such places depends on their being able to reach them as well as on their ability to live in them. Small coastal streams and springs belong to this group, and the common cattle ponds of the midlands and south of England provide such places in immense numbers: in the 6114 acres of the parish of Aldenham in Hertfordshire there are or have been about 170. The dew ponds[2] of the chalk downs are a rather dramatic type of the same thing. They are mostly from 5 to 30 yd. across, seldom more than 2 or 3 ft. deep; they receive water only from the rain or dew which falls in the immediate neighbourhood or which seeps through the soil, and lose it only by evaporation or percolation. These ponds have either been made *de novo* or made out of existing marshy places to which they would all gradually evolve and ultimately become dry land if they were not from time to time cleaned up and dug out. In the form of ponds with free water they have therefore a limited life and the conditions in them are constantly slowly changing. Some of them are derived from primaeval loci; the new ones presumably date from the keeping of cattle in enclosed fields or the extension of sheep farming on the downs and are about 300 years old or younger. Like the flora (**236**) their fauna depends to some extent on their age.

Many of these closed ponds contain an abundant molluscan fauna: it is indeed, I think, true to say that something will be found in all in which a collector would on inspection expect to get Mollusca and in a fair proportion of those which look unpromising. More than 100 years ago Montagu (**35**, p. 90) was impressed at finding *Sphaerium lacustre* "and 1 or 2 others" in a remote closed pond in Wilts., but it was Reid (**36**), in his classical paper "On the natural history of isolated ponds", who first drew attention to the interest and significance of the facts which make it quite clear that many species are carried overland without much difficulty. *Limnaea peregra*, *L. stagnalis*, *Sphaerium lacustre* and *Pisidium* spp. seem to be the species most commonly found in downland dew ponds (**281**) which are often a long way from one

[1] "Closed" was perhaps rather an unfortunate choice, but the obvious alternative "isolated" implies remote from other water which many of the loci in question are not. In the present connection, "closed" means that nothing can get into them without coming overland. In botanical ecology, the word has been in common use to indicate habitats which are full, i.e. in which a new-comer can find no room. It may be that some small ponds are "closed" also in this sense, but the evidence is suggestive rather than conclusive (below, p. 127). Perhaps "discontinuous" habitats would be better.

[2] A great deal of unnecessary mystery has been made about dew ponds. They do not easily dry up because (*a*) they are watertight, (*b*) rainfall is nearly always considerably in excess of evaporation from a free-water surface, (*c*) there is seldom any standing vegetation to increase the water loss by transpiration.

another or any other water: in the majority of those which I have looked at in Wiltshire I could find no Mollusca. The cattle ponds in the parish of Aldenham (**7**, **9**) are much closer together and near other loci which are rich in snails. In 1915, 69 of the 84 closed ponds which survived till 1925 contained Mollusca of 18 species, the total occurrences being 173; the number of sorts per pond varied from 0 to 8 with an average of 2·1. The most frequent species were *Planorbis nautileus* (32 ponds), *Limnaea peregra* (26), *Ancylus lacustris* (18), *Sphaerium corneum* (15), *Sph. lacustre* (15), and *Planorbis fontanus* (12); *Limnaea palustris* (2), *L. stagnalis* (6), *Planorbis albus* (8), *Pl. complanatus* (3), *Pl. vortex* (3), *Pl. spirorbis* (3), *Pisidium cinereum* (2), *P. milium* (9), *P. nitidum* (3), *P. obtusale* (5), *P. personatum* (7) and *P. subtruncatum* (4) were also present. Figures such as these do no more than systematise the experience of all collectors and they represent the accumulation of many years of dispersal.

A re-examination of the same ponds in 1925 gives us perhaps some idea of what is going on now. Only 65 of them yielded Mollusca; there were 64 disappearances and 93 fresh appearances (mostly *Planorbis nautileus*, *Pl. fontanus* and *Ancylus lacustris*), so that the total number of occurrences had risen to 202. Making some allowance for the imperfections of collecting, these data indicate that transport overland is going on at a considerable rate: on the average each pond got one new species every 9 years.[1] Other evidence comes from *Paludestrina jenkinsi* (below, p. 140), which in the last 40 years has invaded the fresh waters of this country from its original estuarine habitats and is now a common inland species. It hardly occurs in stagnant water, and theoretically it might have reached most of its loci by crawling up the rivers, streams and canals. But it is frequent in little springs and trickles on the coasts, e.g. of Devon and Cornwall, which are in effect as isolated and "closed" as a dew pond, and it has reached the islands of Skokholm and Skomer (**37**, **228**) off the Pembroke coast, Orkney (**38**) and North Uist (A. R. Waterston), as well as remote districts in the west of Ireland. *Elodea* is also a useful analogue, for in this country it spreads by the dispersal of pieces of the plant. Introduced about 1847, it got all over England in the next 25 or 30 years (see the map in **39**, p. 393) and is not uncommon in closed ponds. It is easily killed by drying—more easily than most snails—and one cannot doubt that the agent which spreads it would be equally effective in dispersing Mollusca.

This evidence all goes to show that certain species at any rate are easily and freely dispersed. Unfortunately many interesting kinds are seldom or never found in closed ponds, nor can they live there if they are put in, so that one cannot tell whether they are easily transported or not. For *Planorbis corneus* we have definite evidence (**8**, **40**) that transport is difficult though it is not very easy to see why. Laver (**41**) round Colchester noticed the paradox that though it was naturally confined to the river system the largest specimens he had seen were in a water butt. It is roughly true that the species "never"

[1] Nelson (**224**) describes the addition of 6 species to a pond fauna of 4 in about 20 years.

occurs spontaneously in small closed ponds, though it has been successfully introduced into a good many by aquarists in England and Ireland (**116**), especially in its decorative albino form (**183**). It was certainly absent from the Aldenham ponds until I introduced it into a number in 1917, since when it has flourished and still abounds, without any further, spontaneous spread from these secondary loci: Welch (**179**) notes similarly that it has not spread from a locus in Sligo to which it was introduced 30 years ago. It is evident in this instance that there is little difficulty about oecesis if transport can be achieved. Reid noticed that the operculates were not found in closed ponds and this is nearly true. As Prashad (**269**) and Thomasson (**239**) point out, it is hard to see how *Paludina* could be carried about, and it never occurs in closed ponds unless it has been put there by man, e.g. in the King Lane pond at Leeds or in the Manchester pits (**84**) or in a garden pond at Hereford (**28**). But there is no obvious difficulty in the transport of young *Bithinia* or *Valvata*, and *Bithinia tentaculata* does occasionally occur in marl pits in Cheshire (**85**) and Kent. *Anodonta* and *Unio pictorum* rarely live in closed loci: where they do they were probably introduced as glochidia on fish (generally carp) with which many ponds were stocked when the standard of life was lower and people were glad to eat such tasteless food.

The *means of transport* were very fully discussed by Kew in 1893 (**73**), and I do not think anything has been seen since which adds anything really new to his survey, though various fresh examples of snails in transit have been observed. There is also much interesting information in Ridley's book (**127**) on the dispersal of plants, and in Arber (**166**) and Peacock (**231**). The chief agents are, I believe, birds and especially wild duck, which may have bivalves nipped on their toes or gastropods sitting on their legs or any small snails in mud on their feet or beaks or in wisps of weed round their necks. Insects may also play a part over short distances, and if whirlwinds can produce showers of fish (**165**) they can no doubt distribute snails as well. Stelfox (**80**, **241**) thinks that more consideration should be given to the possibility of snails and small mussels crawling overland through wet vegetation.

(*e*) *Competition*

As I pointed out in my previous paper (**132**) there is little or no evidence that interspecific competition is a factor of any importance in determining the occurrence of land Mollusca. With the fresh-water species the position is rather different: there are facts which suggest competition though they are not conclusive.

(*a*) It is, I think, true that other things (water, climate, etc.) being equal, a large habitat is likely to contain more species than a small one, and going from one locus to another one gets the impression that, for example, a cattle pond 10 yd. across may be "full" in the sense that there is no room for fresh species, the delicate young of which would presumably be more sensitive to

crowding than the established population. There may of course be other reasons for this than competition: a large locus contains a greater variety of subhabitats than a small one and the visits of transporting agents are probably more numerous, i.e. there is more prospect of a snail reaching the larger place and of finding congenial conditions when he gets there. But facts such as the following are suggestive. In 1915–25 there were in the Aldenham ponds 18 species which might, as far as one could judge, each have occurred in any one of 40 small closed ponds of a favourable complexion: but in 1925 the distribution was as follows:

Kinds of Mollusca	...	1	2	3	4	5	6	7	8
Number of ponds	...	2	9	6	9	6	4	3	1

The most abundant species were *Planorbis nautileus* (26 ponds), *Pl. fontanus* (24), *Ancylus lacustris* (19), *Limnaea peregra* (17) and *Sphaerium corneum* (17). From this we may judge that such a pond becomes fairly "full" when it contains 5 or 6 of the species which are available in the immediate neighbourhood and able to live in such places. It also seems significant that 20 ponds which in 1915 had one or two sorts each had by 1925 made a net gain of 37 occurrences, whereas 11 ponds which started with 4 or more species per pond showed a net loss of 3. Two larger loci near-by—a reservoir and a backwater of the Colne—each showed 13 of the pond species as well as their own special kinds. Apart from size, both of them are in general more favourable places for Mollusca than the cattle ponds, and we have to bear in mind the general rule that competition is more likely to be effective under indifferent or bad conditions. Large loci of a good kind (below, p. 171) may contain nearly but never quite all the possible species, and it would perhaps be unreasonable to expect a complete galaxy. As J. C. Bellamy (**26**, p. 315) said as long ago as 1839, in a pioneer work on animal ecology which deserves to be better known, "I believe no instance can be adduced where the Fauna of a locality accords so precisely with its physical conditions as to include all those creatures generally found in such spots, and to exclude those generally absent from the same", and Elton (**42**, p. 22) has emphasised the same truth.

(*b*) Some one species, generally *Limnaea stagnalis* or *L. peregra*, sometimes occurs in such profusion in a small locus that it seems hardly credible that there can be enough room and food for many other species, especially those with much the same habits: bottom dwellers with different food requirements such as *Sphaerium* and *Pisidium* are presumably less affected. After all, food shortage can be very obvious in an aquarium: a water volume of 2 litres with a good stock of *Elodea* is just enough for the full growth of one or perhaps two *Limnaea peregra* and does not suffice for even one *L. stagnalis*, *L. auricularia* or *Planorbis corneus*. A small pond of 200,000 litres or so may therefore be presumed to have its limiting capacity, though I do not think that it is often reached. Stelfox, Welch and others (**100**, **103**) have commented on the

disappearance of other species when *Paludestrina jenkinsi* appears in and overruns a locality.

(*c*) The land snails which occur in the bad loci which contain only a few sorts flourish equally in the best places which have many: with the possible exception of the calcifuge *Zonitoides excavatus* there is no evidence that any species is excluded from desirable loci by the "pressure of competition". This is also true in the main for the water Mollusca, but there appear to be several species which are driven to live in "oecological slums" with few or no companions and which are absent or rare in good places. The particular variety of slum is that provided by ponds, pondlets and ditches which hold water only in the winter and spring and go dry in any but the wettest summers: *a priori*, and by demonstration, these are not acceptable to most Mollusca, and they are deficient in plants and so in humus (**9**); they are "bad" places in the sense of being inadequate, not poisonous.

Limnaea glabra. Since the times of Müller (**43**, p. 136) who says, "in pratis humidis, ubi aquae vere stagnant", and of Montagu (**35**, pp. 396, 590), who found it only "in a splashy place by the road side, half way between Fowey and Looe in Cornwall", it has been generally recognised that *L. glabra* characteristically occurs in mean places where few if any other Mollusca care to live—shallow grassy ditches and ponds which usually dry in the summer, sometimes in marshes. It is often, probably generally, the only gastropod present: the available records are unfortunately very imperfect as regards *Pisidium*, and I imagine that some of these (*cinereum*, *personatum*, *obtusale*) would frequently be present. It is never found with a rich or even a respectable snail fauna, and the flora seldom goes beyond *Glyceria*. If other snails are present, they are restricted to the few species which can tolerate the conditions, i.e. *Limnaea peregra*, *L. palustris*, *Planorbis spirorbis*, *Physa hypnorum* and the *Pisidium* I have mentioned, less commonly *Planorbis nautileus* and *Sphaerium lacustre*. Thus Nelson (**44**), in some interesting papers on its occurrence round Birmingham and in Yorkshire, gives the following companions (neglecting *Pisidium*): (*a*) *Planorbis spirorbis*, (*b*) *Pl. spirorbis* and *Physa hypnorum*, (*c*) *Planorbis spirorbis* and *Limnaea peregra*, (*d*) *Planorbis spirorbis*, *Limnaea peregra* and *L. palustris*, (*e*) *Planorbis spirorbis*, *Physa hypnorum* and *Limnaea palustris*, and finally (*f*), which this experienced collector says is unique in his experience, with *L. peregra*, *Planorbis complanatus* and *Pl. contortus*. Common repute associates it particularly with *Physa hypnorum* and *Planorbis spirorbis*, as e.g. Morehouse found (**270**) but without, I fancy, taking sufficient account of the frequency with which it occurs alone. Richardson (**271**) found it with *Limnaea peregra*, *Planorbis nautileus*, *Pl. spirorbis*, *Sphaerium lacustre* and *Pisidium* sp.. Hey (**272**) with *Limnaea peregra* and (which is rare) *Sphaerium corneum*. Blackburn (**160**) with *Planorbis spirorbis* and *Pisidium personatum*; Alkins (**50**), Adams (**64**) and Evans (**251**) note its concurrence with *Sphaerium lacustre* and Alkins says that generally *Pisidium personatum* is its only companion. I also have notes of its occurrence, without

any other snails, with *P. cinereum* (**45**), with *P. cinereum* and *P. personatum*, with *P. obtusale* and *P. personatum* and with *P. personatum* (**46**). Geographically (Fig. 56) it occurs in a few places in Scotland as far north as Perth (**47**), in one place in Ireland and fairly generally in the northern half of England, in some parts of which (e.g. the Cheshire plain and parts of north Staffs.) it is not uncommon. In the southern half it is generally very rare though rather frequent in the New Forest in shallow ponds and temporary running ditches: mean ditches and drying ponds are common enough everywhere, so there must be some other factors to make a place suitable beyond a propensity to go dry in summer. Though it does not extend far north it has been found at considerable altitudes: 1100 ft. in Stafford by Alkins (**46**), 900 ft. in Edinburgh by Evans (in **47**) and 900 ft. on Breidden Hill in Montgomery by Oldham with *Limnaea peregra*, *Planorbis spirorbis* and *Pisidium personatum*.

Nelson had the impression that it is particularly frequent on commons, past and present, and if I were trying to summarise the characters of the places in which it is found I should say that it affects areas where the ground is harsh and poor, where the neighbouring vegetation is not luxuriant, where few land Mollusca will be found and where arable farming is at a minimum, i.e. the places which have longest been left as waste or common land because they have been little worth cultivation. Correspondingly, roadside ponds are rather common habitats which are in undisturbed and therefore well-leached soil. Laver (**41**) for Essex says "especially on gravelly soils" on which he never found *Limnaea stagnalis*. And, though it is not found in moorlands, it may be surmised from this that the water would be found deficient in salts: the only analysis I have (from Boscastle in Cornwall) showed very soft water (7 mg. calcium per litre), and I know of no natural occurrence in water which might be presumed to be hard. Butcher (**229**) says the New Forest streams are poor in mineral salts, and Ashford (**60**) comments on the erosion and decollation of *Bithinia tentaculata* there. The shell of *Limnaea glabra* is often decollated, and Beeston (**128**) suggests that they eat one another's shells for want of lime.

Experimentally in aquaria I have bred *Limnaea glabra* without any difficulty in both hard and soft water. Some from Leeds (which I owe to H. W. Haywood) were carried on for 2 generations in water with 6, 30, 60 and 100 mg. calcium per litre without any obvious difference, the figures representing the range from very soft natural waters to the exceptionally hard London supply. Other examples from Edinburgh (from A. R. Waterston) went on for 5 generations in Radlett water (calcium 60). But I am doubtful whether such experiments are conclusive except to show that it can live in hard water and that summer drying is no necessity as it is with some Crustacea or the seeds of *Alisma*. As others have noted (**59**, p. 135) it is fond of climbing out of the water in aquaria and often stops out till it dies. In nature, as might be expected, it breeds when its habitats contain water, i.e. in February or March.

Planorbis spirorbis belongs to the same group and has a distinct addiction to drying ponds, marshes and other bad places. It is far commoner than

Limnaea glabra and extends throughout Britain (Fig. 8). The data for the Aldenham loci seem to be characteristic and instructive. In 1915 out of 98 ponds which contained Mollusca it was found in 5, all of which went dry each summer: its companions were *L. peregra* (thrice), *Pisidium obtusale* (twice), and *P. personatum* (once). One pond was soon afterwards destroyed: *spirorbis* disappeared from another in 1916, from another in 1917 and from another in 1919, though in this last it had been so abundant that I took 620 specimens in one sweep of a small scoop. In 1921 it could be found in only one pond in the parish. However, in 1925, it was found sparsely (with *P. milium*) in another pond from which it had gone in 1926, and between 1923 and 1926 it appeared in 3 others, in 2 by itself, in the other with *Limnaea peregra*, *Planorbis nautileus* and *Pisidium obtusale*: from one of these it had gone by 1927 and from the 2 others by 1932. So that at the present time (1934) it again occurs in only one locus—a shallow trampled cattle pond 6 yd. across with *Glyceria* and *Juncus* which dries on the least provocation and in which *Planorbis spirorbis* and *Pisidium obtusale* have been abundant since 1915. It seems evident from this narrative that *spirorbis* is moved about from one place to another without much difficulty, and that it is far from happy in many of the loci to which it gains entry. Now during this period of 19 years there have been within about 1½ miles of the 9 *spirorbis* loci, all of which were drying ponds, at least 51 ponds which did not dry out even in 1921 or 1933 and which contained such a number of Mollusca (above, p. 125) that one could not doubt that they were fairly good habitats: but *spirorbis* has not been found in one of them. It is difficult to resist the conclusion that it lives in these bad places because it is excluded from the better habitats by the competition of other Mollusca. This fits in well with the fact that when we pass to roomier loci than cattle ponds we find *spirorbis* again and often in company with many other species. Thus in my own neighbourhood it lives freely in a large reservoir with 16 other species and it is not uncommon in such places, in canals, draining ditches, quiet river loci and the like, which have quite rich faunas. Thus Wood (**48**) found it in 3 of 11 midland lakes with such characteristic running water species as *Bithinia tentaculata* and *Physa fontinalis*. Like *Limnaea glabra*, it does not occur in the average good small pond, but unlike that species it can live with other species if the locus is large enough.

Pisidium personatum also prefers bad places. It is a widespread and common species in miserable loci and sometimes in wet places on land, and frequently occurs by itself. As Stelfox (**49**) points out it is not often found in good habitats, and Alkins (**50**) in his survey of the Oakamoor district found that it was restricted to ditches and marshes and was most frequent in those which dried in the summer; Favre (**51**) finds the same in Switzerland. And, particularly interesting, it lives in the depths of Rostherne Mere, Lake Windermere (C. Oldham) and the Lake of Geneva (**51**), to which only *P. conventus* of the other species of the genus and only *Limnaea peregra* of the other Mollusca

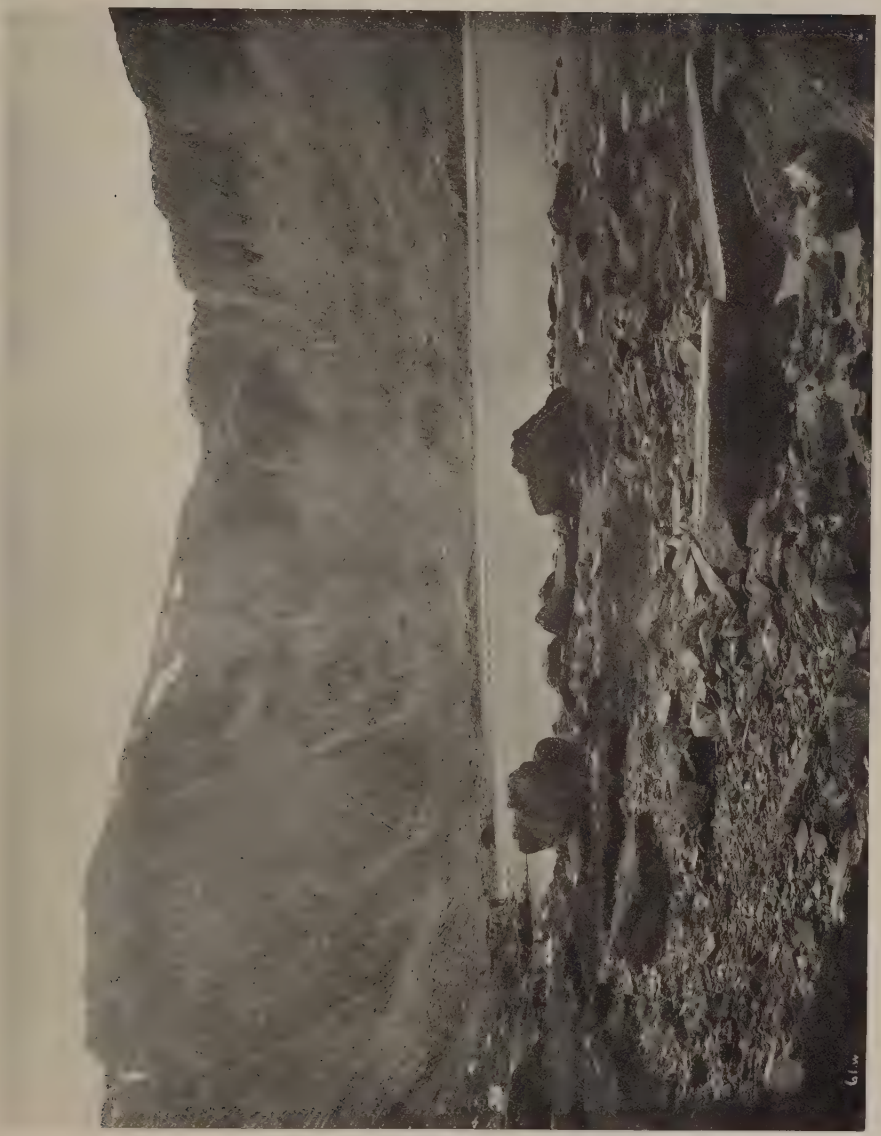


Photo. Abraham, Keswick

Phot. 1. Llyn Idwal, Carnarvonshire. A characteristic soft water lake, calcium 3 mg. per litre; 1223 ft. above sea level; relatively sheltered. the surrounding country rising to more than 3000 ft. Mollusca: *Limnaea peregra*, *Ancylus fluviatilis*, *Pisidium cinereum* and *P. lilljeborgii*. Above and to the right is the patch of calcareous ground where *Helix nemoralis*, *Clausilia rugosa* and other mollusca live with calcicole plants at 1800 feet (**132**, p. 10).

which live in this large water penetrate. It may be that *Pisidium obtusale* should go in the same category: it lives in poor loci, often by itself though seldom with *P. personatum* (below, p. 138), but its requirements are difficult to specify and its status remains indeterminate.

Physa hypnorum. To *Limnaea glabra*, *Planorbis spirorbis* and *Pisidium personatum* common opinion would add *Physa hypnorum*, but it seems doubtful whether it is really a slum dweller. It is quite true that it often occurs in shallow grassy drying pools[1] (including ponds among sand dunes (**219**)), temporary spring flashes, etc., and frequently with *Planorbis spirorbis* and sometimes *Limnaea glabra*, and Jenyns (**52**) remarked long ago on its curious habit of suddenly appearing and disappearing: it has these same habits throughout its extensive palaearctic range, in which, in Siberia, it lives nearer the Pole than any other pulmonate. Though it has been recorded at one time or another for all except 5 of the English counties, it cannot be called common, and many collectors would be hard put to it to lay their hands on live specimens on demand. But I feel uncertain about its having an actual preference for bad loci or an intolerance of companions, for examples to the contrary are easy to find. It lived for a while in a draining ditch near Watford with *Limnaea palustris*, *Planorbis corneus*, *Pl. complanatus*, *Pl. vortex*, *Pl. spirorbis* and *Bithinia tentaculata*; Stelfox (**54**) records it in Arland's Lough, Donegal, with *Limnaea peregra*, *L. auricularia*, *Planorbis nautileus*, *Pl. spirorbis* and *Pl. glaber*; Ellis (**55**) in Saddington Reservoir, Leicester, with *Limnaea peregra*, *L. stagnalis*, *Planorbis fontanus*, *Bithinia tentaculata* and *Sphaerium lacustre*. These would all count as "large" loci, but in two Lancashire ponds Davies (**56**) found it with *Limnaea peregra*, *L. stagnalis*, *Planorbis fontanus* and *Pl. nautileus* and Jackson (**57**) with *Limnaea palustris*, *Planorbis carinatus*, *Pl. vortex* and *Pl. spirorbis*. I suspect therefore that *Physa hypnorum* may not be an example of competitive seclusion but may more properly be classed with the next group which contains 4 species which are notoriously apt to be found in inferior loci because they happen to be able to tolerate the conditions and which are as common or commoner in good places with plenty of companions. The occurrence, for instance, of *Sphaerium lacustre* in dried ponds has often been commented on, and it has been stated (**59**) that the valves fit particularly closely though according to my own experiments it is no more resistant to drying in air than *Sph. corneum*; Collinge (**58**) says that it burrows exceptionally deeply (10–14 in.) in the mud. But the idea that it prefers such places is illusory and arises I think from our tendency to remember the dramatic discovery of many little mussels in a dried-up dew pond on the downs and to forget the occurrence of the same species in more conventional loci. In fact *Sph. lacustre* is quite common in many good places—ponds, rivers, canals—as well as in bad ones, and there is no evidence that it is driven into drying

[1] Dr K. B. Blackburn tells me that it is fond of the alga *Tribonema* (which other snails are not) and eats it freely.

ponds by competition. Similarly, *Planorbis nautileus* is frequently found in drying ponds especially if they are examined in spring when they contain water. But in our local ponds it occurred in 26 of 42 ponds which did not dry and in only 14 of 42 drying ponds[1] and this is in accord with general experience. *Limnaea palustris* is another species which lives sometimes in surprisingly dry places; Adams (**59**), for instance, calls it "amphibious", Ashford (**60**) says it may "lead an aerial life during summer", and Kew (**61**) mentions it in temporary winter water. In Aldenham I have watched it for 17 years (including the 1921 drought) living in thick grass by the roadside, where it got no more water than ran off the road: it was always plentiful until the place was destroyed in building operations. But its toleration of these conditions is in no way compulsory, for it is definitely more common in a variety of good habitats. The same appears to be true of *Pisidium cinereum* which can tolerate drying loci but is much more frequent in better places.

Of these 9 species which can put up with drying ponds, none is restricted to such places as are *Planorbis umbilicatellus* and *Pl. campestris* in northern Canada (Mozley), where melting snow produces ephemeral ponds each year in the same place in which *Limnaea palustris* and *Physa hypnorum* are frequent with *Sphaerium occidentale*, analogous to *Sph. lacustre* (**17**, **18**). Mozley (**250**) gives a good account of the flora and fauna (including 7 molluscs) of a Canadian pond which held water for less than 3 months in each year.

3. The habitats of the various species[2]

(*a*) *Bivalves*

The four large mussels—**Anodonta cygnea* (Fig. 36), **A. anatina* (Fig. 37), **Unio pictorum* (Fig. 45), **U. tumidus* (Fig. 46)—live in slow rivers, canals, large draining ditches, lowland lakes, reservoirs and large ponds, mostly running habitats though *Anodonta cygnea* and *Unio pictorum* live in some closed marl pits in Kent and *Anodonta cygnea* in marl pits near Manchester (**175**). The deliberate introduction of fish for angling or in times past for food probably explains why *Anodonta* and *Unio pictorum* are so common in reservoirs and ornamental waters, though they are sometimes put in for their own sakes (**174**) and were at one time eaten in Ireland (**181**; **247**, p. 31) and in the Fens (**243**). Thomasson (**239**) attaches special importance to sticklebacks on which he finds the glochidia. Only *cygnea* lives in Ireland, and in Great Britain it has been recorded as far north as Banff; *anatina* extends as far as Caithness, and the two *Unio* are restricted to England. This distribution is probably due in part to the relative rarity of suitable habitats in the north and west as well as to historical and climatic factors. Their essential needs are fish on which they can pass their early parasitic phase and incidentally travel about and a firm muddy bottom in which they can imbed themselves. Why they spend so much of their time two-thirds sunk in the mud I do not know: it seems an extravagant precaution against being swept away by any ordinary current. But a bottom suited to such a life is obligatory. They will not

[1] The corresponding figures for *Sphaerium lacustre* are 15 and 2 but I doubt whether these are really representative.

[2] In the following catalogue the species which are able to live in quite soft water are marked †, calcicole species ** and those which appear to need at least a moderate amount of lime *: the evidence is discussed in more detail below (p. 148).

live either on a hard stony or gravelly bottom or on one which is covered with a thick layer of soft humus in which they would have to disappear before they found firm ground: hence most closed ponds are unsuitable. The four species have similar tastes and may all occur together. *Anodonta anatina* seems to have rather more preference for rivers than *A. cygnea*, and *Unio tumidus* is distinctly the least common and has the most restricted geographical range: it needs fresher, cleaner water than the others and may be a river species which has extended into canals: Lowe (**243**) failed to get it to live in captivity, though *Unio pictorum* did well. *Anodonta cygnea* with or without *Unio pictorum* sometimes abounds in lakes without any pulmonates or operculates (**273**), which illustrates the dependence of the bivalves on the bottom and of the other groups on the water and vegetation.

**Pseudanodonta rothomagensis* (Fig. 61) (if that be really the correct specific name of the English form) is a river species occurring in the Thames and Severn basins and in some of the midland and Yorkshire canals.

The pearl mussel †*Unio margaritifer* (Fig. 14) lives in a well-defined river habitat, though it is a little difficult to specify the essential qualities. As Adams (**59**) points out it occurs only to the north and west of a line from Scarborough to Beer Head,[1] and a full account of its history and distribution is given by Jackson (**71**). It lives in the R. Exe, and passing thence east and north along the coast its next locus is the Whitby Esk in Yorkshire: travelling the other way it is found in Cornwall, all up the west coast and generally in Scotland north of Stirling, in Shetland, Lewis, Isle of Man and generally in Ireland, except in the central limestone plain and the Shannon basin. It is absent from the whole of the midlands and south-east of England. A typical locus is a quick running river up to 3 or 4 ft. deep with a mixture of boulders, stones and sand; it can burrow in fine gravel and particularly likes the sand which accumulates behind large stones: it also lives in the lakes (e.g. L. Earn) through which such rivers flow. Most of its habitats are places in which fishermen would expect to get trout and hope for salmon, though it occasionally (**194**) occurs in meagre streams. As it happens, most of the characteristic rivers contain soft water, and the areas in England and Ireland where it does not occur have hard water. Hence the belief, which I have advocated more than once (**7**, **133**), that soft water is the main factor in determining its occurrence.

There is no doubt that the great majority of its habitats contain soft water, and the following list[2] contains such recent analyses as I have been able to get. It is unrepresentative because I have neglected such districts as the west of Scotland (where all the rivers north of the Clyde must surely be soft) and gone out of my way to get samples from known habitats of the mussel in calcareous and dubious districts:

Glengarriff R. (Cork)	1	R. Teign (Devon)	3
R. Spey (Inverness)	2	R. Derwent (Westmorland)	6*
R. Dee (Bala)	2–4	R. Esk (Yorks.)	6
R. Irt (Westmorland)	2*	L. Leane and rivers (Kerry)	7–11
R. Conway (N. Wales)	3	R. Exe (Devon)	10
L. Lubnaig (Perth)	3	R. Taw (Devon)	11

* By the kindness of Dr W. H. Pearsall (see **291**).

[1] "If a line be drawn from Hull to Gloucester and then on to Plymouth, it can be said roughly that all the country to the east and south of it was for Parliament, and everything to the west and north for Charles." *Wales*, by W. H. Davies, 1925, p. 170.

[2] The figures are milligrammes of calcium per litre, i.e. parts per million, which I have always determined by the method given by Thresh and Beale (**148**). Divided by 4, they give approximately the total hardness expressed on the customary scale of parts of $CaCO_3$ per 100,000, and to have a uniform terminology I have converted the hardness figures of the literature to the calcium scale by the same factor, making the necessary correction if they are given in the older scale of grains per gallon (=parts per 70,000). But what is meant by "hardness" or "lime" is not always clear.

R. Tamar (Cornwall)	14	R. Lune (Lancs.)	30
R. Blackwater (Cork)	15†	R. Rede (Northumberland)	32
R. Ithon (Radnor)	17	R. Usk (Monmouth)	49, 51‡
R. Teme (Clun)	19	R. Nore (Queen's Co.)	79
R. Wye (Hereford)	15–33		

† From E. O'Mahony and A. W. Stelfox.
‡ From Dr H. W. Catto: a third sample higher up 12 years later gave 30.

In contrast with these I give a few figures I have collected which seem to be representative of the rivers in the south of England draining from calcareous strata which do not contain the pearl mussel:

R. Granta (Cambridge)	113	R. Avon (Salisbury)	85
R. Kennett (Suffolk)	115	R. Test (Hants.)	89
R. Gade (Herts.)	104	R. Frome (Dorchester)	70
R. Colne (Herts.)	107	R. Piddle (Weatherbury)	90
R. Thames (Staines)	90	R. Stour (Blandford)	85

West and north the hardness becomes rather less, e.g. R. Axe (Devon) 47, R. Otter (Devon), 37, R. Tees 32 and R. Tyne 34–36: none contain *U. margaritifer*.

The significance of soft water is also supported by the facts: (*a*) it occurs in the upper part of the Dee, above Corwen, where the water is soft (Ca 4) and not in the lower parts where it becomes as hard as 28 (Shrubsole, **65**, **148**); (*b*) similarly in the Teme it lives at Clun, where a sample gave 19, but not below near Ludlow where the hardness rises to 29–35; (*c*) it is common in the Herefordshire Wye (about 20) but not in its tributaries Lug (49), Arrow (41) or Monnow (37). Frierson (**66**) says that it does not occur in calcareous waters in the United States and Geyer (**67**) that it affects soft water in Germany. Further evidence in the same direction was given by McKean (**68**), who found that specimens from the R. Don in Scotland soon died when they were put into the chalky R. Wandle in Surrey, and by Haas (**69**) who says that his specimens died at once when they were transferred from soft to hard water.

The case for soft water is up to a point impressive, but it is difficult to put on one side the instances of the Usk and the Nore or to agree with Phillips (**70**) that the well-grown thick shells from the latter place are a new species. When too I tried Haas' experiment with specimens from the Wye[1] I found (**71**) that they lived happily in various hard waters with calcium 50–130 and finally in the Herts. Colne (Ca about 100) for several months till the winter floods carried them off. It is thus almost equally easy to argue that the thing that is requisite and necessary is a quick-flowing cool river with clean water and the right kind of bottom, and that it is as it were a physiographical accident that such rivers are nearly always soft, though I should have judged by the look of them that such southern calcareous rivers as the Test, Itchen or Otter would have been agreeable to *margaritifer*. It can hardly be the high summer temperature which excludes it from the south-east of England, for it is equally absent from the Shannon basin which is as cool as Wales or Cornwall. The natural host for the glochidia, which are very small and attach themselves to the gills, is the trout (**109**), which is common enough throughout Britain in both hard and soft water: minnows (**110**) also do well and are generally available except in the north of Scotland and parts of Ireland (**72**). Perhaps the solution of this very interesting question may come when someone discovers where the young mussels live after they fall off the fish till they are about 2 in. long—a matter of several years: at present this is quite unknown.

Dreissena polymorpha (Fig. 44) is closely connected with commerce and is found in docks, canals, rivers and reservoirs, anchoring itself to any hard surface by its byssus; it can also live in water mains (**238**), though as it preserves the marine habit of a free-swimming larva its maintenance in running water must be rather precarious, and it is not clear that it would survive in fresh water in this country under natural conditions. It is fond of

[1] It would have been better if they had come from a less calcareous river.

fixing itself to *Anodonta* and *Unio*, and in their turn the fry may be incorporated in caddis cases (Swanton); the free locomotion of the young mussels has been described by Tate (**247**, p. 24) and Oldham (**248**). Kennard (**74**) records it as a fossil in London and Oxfordshire. It subsequently died out and in modern times was first found in 1824 in the London docks and within 20 years was known to be present in Scotland and in England from Lancs. and Yorks. to Devon; Kew (**73**, p. 210) gives a full account of its early history.

†*Sphaerium corneum* (Fig. 15) is widely spread throughout Britain in most kinds of waters, running and stagnant; other species are likely to be found with it, and it is a useful indicator of pretty good molluscan conditions: it can live in brackish water and occasionally in mountain lakes (e.g. L. Kinardochy, Perth, 1200 ft.), so that it has a wide range. It does not like dirty water nor does it live in drying ponds and streams.

†*Sphaerium lacustre* (Fig. 16) is rather less widespread and strangely rare in Ireland and tends to be found more in stagnant and less in running water and often by itself or with few companions in inferior loci including dew ponds and drying ponds (above, p. 131) in which *Sph. corneum* does not occur. In my analysis of the Aldenham ponds (**7**) *Sph. corneum* occurred in 18, *Sph. lacustre* in 13 and both in 5; *Sph. corneum* was concurrent with *Limnaea stagnalis* and perhaps *Planorbis complanatus*, *Sphaerium lacustre* with *Ancylus lacustris*, which to a collector perhaps expresses as well as anything else the difference in their tastes. Lukis says (in **246**, p. 12), and I have the same impression, that it is more active than *Sphaerium corneum*, especially when young, and crawls up into the plants more, which may aid its dispersal.

***Sphaerium rivicola* (Fig. 47) is a central English species as far north as Yorkshire: it fails in west Wales, south-west England and East Anglia. It lives in quiet rivers and canals, in deeper water than *Sph. corneum* (**176**).

Sphaerium* (*pallidum*) *ovale* (Fig. 48) was discovered as a new British species on May 17, 1856, by J. Rouse in the Grand Junction Canal at Kensal Green (75**), and has subsequently been found in Oxford, Gloucester, Northampton, Warwick, Worcester, Stafford, Shropshire, Montgomery, Cheshire, Lancs. and Yorks.: it lives in great profusion in some of the Manchester canals where it was first found in 1860 (**295**). All the trustworthy records (Roebuck MS.) are for canals except the Foss and Ouse at York which are canalised rivers and in which incidentally all four species of *Sphaerium* live together (**81**). It is unknown in Europe and is not the continental *Sphaerium ovale* (**77**) which has no relation to canals. It does not climb up the walls and plants as *Sph. corneum* and *Sph. lacustre* sometimes do.

Our knowledge of the 15 British species of *Pisidium* has been revolutionised in the last 20 years by the work of C. Oldham, R. A. Phillips and A. W. Stelfox, who have put the systematics of a difficult genus on a firm basis and by their intensive field work have given us as much knowledge of their distribution and habitats as we have for any other Mollusca. Unfortunately it has not been easy for others to join in what has proved to be an exceptionally interesting oecological enquiry because there is no printed account through which fresh workers might learn their species; most collectors therefore are unable to identify the more critical kinds and so neglect them. Some of them have very definite habitats, and I am indebted to Mr Oldham for the following summary.

As the species are as much (or more) affected by the nature of the bottom in which they live as by the character of the whole habitat, their preferences cannot always be described in ordinary terms and what is one locus as far as, for example, *Limnaea peregra* is concerned, may contain a number of *Pisidium* loci. The species may therefore be extremely localised in a habitat, and collecting them satisfactorily is something of a special art (**78**). 10 of the species occur throughout Britain, so that their habitats can be considered without any geographical confusion.

**P. amnicum* (Fig. 38): general in England, infrequent in Scotland (to Perth), west Wales and west Ireland: clean running water in rivers, streams, canals and lowland lakes.

†*P. cinereum* (*casertanum*) (Fig. 17): general: in all kinds of habitats, good and bad, the most catholic species.

†*P. conventus* (Fig. 18): mountain tarns, mostly high and cold, in north Wales, north Scotland and Kerry (**78**, p. 275): dredged from 400 ft. in L. Ness.

**P. henslowanum* (Fig. 39): distribution much the same as *amnicum* but extends to Shetland: running water, rivers, canals, lakes and running ponds, occasionally in marl pits.

†*P. hibernicum* (Fig. 19): general but less common in the south: mountain lakes, canals, rivers and streams; rarely in closed ponds.

†*P. lilljeborgii* (Fig. 20): north-western: in clean gritty sand or silt, not in mud, and characteristically in mountain lakes both at high altitudes and near sea-level; hence mostly in soft water: it lives, however, in hard water in Malham Tarn and Gormire in Yorks., L. Rea in Galway and in Anglesea (**142**), and the determining factor seems to be the nature of the bottom rather than of the water: analogous to *Unio margaritifer* (above, p. 133).

†*P. milium* (Fig. 21): general: ponds, rivers, canals, tarns, not in bad ditches or swampy places and not so ubiquitous as *cinereum*.

†*P. nitidum* (Fig. 22): general: much as *milium*, not in bad places.

†*P. obtusale* (Fig. 23): general: small ponds, stagnant water, peaty holes; not usual in rivers, streams and canals; often by itself.

†*P. personatum* (Fig. 24): general: stagnant water, puddles and temporary ponds, sometimes in wet places on land, prefers bad places (above, p. 130) and extends from the bottom of L. Windermere to 3000 ft. in Perth (**79**) and St Brendan's Well at 2700 ft. on Brandon Mt. in Kerry, which is "probably the highest possible habitat for a fresh-water shell in Ireland" (**80**).

†*P. pulchellum* (Fig. 25): general but not common: it likes mud with clean water as in running ditches and slow streams, sometimes in lakes and ponds.

†*P. subtruncatum* (Fig. 26): rivers, canals, lakes, draining ditches, also in ponds; very similar to *nitidum*.

***P. supinum* (Fig. 50): mud in rivers, mostly large ones (e.g. Thames, Severn, Wye, Trent, Teme, Ouse, Dee) and canals from Somerset and Surrey to Yorks.: not in Wales, Scotland or Ireland.

***P. tenuilineatum* (Fig. 51): rivers and canals in Thames basin, Northampton and Shropshire.

***P. torquatum* (*moitessierianum*) (Fig. 49): in mud in rivers and canals Cornwall, Wilts. and Surrey to Yorks., and in Ireland; very small and liable to be overlooked.

Mr Oldham has also with great generosity put at my disposal his careful records of his own collections of *Pisidium* from 466 loci scattered from Cornwall to Shetland with some in Ireland. These are the result of deliberate searching for *Pisidium*, not of casual collecting, and they are unrepresentative only in that the various habitats were not examined in proportion to their frequency, and a good deal of the work was directed to the discovery of rare or ill-known species such as *lilljeborgii* and *supinum*. Hence mountain lakes appear in excess and trivial lowland loci in defect of their actual relative abundance, and the figures in the last column of Table 1 do not give an accurate idea of the relative abundance of the different kinds. Otherwise Table 1 tells its own tale about the species found in the various kinds of habitats and Tables 2 and 3 give the concurrences[1] of the species with one another.

These records also show that *cinereum*, *hibernicum*, *lilljeborgii*, *milium*, *obtusale*, *personatum* and *conventus* can live at over 2000 ft., and that *nitidum* is not very rare at over 1000 ft., and exceptionally *subtruncatum*, which Stelfox (**80**) says does not live at that altitude in Ireland: from other sources (below, p. 157) we have a single occurrence of

[1] I have already explained why "association" conveys rather undesirable implications when the only thing which brings species together is a liking for the same type of habitat.

amnicum at 1250 ft., but *henslowanum, pulchellum, supinum, tenuilineatum* and *torquatum* are normally lowland species. By analysis or implication, *supinum, tenuilineatum, torquatum, henslowanum* and *amnicum* (i.e. the southern species) are addicted to hard water, whereas the other 10 can live in very soft water and, except *conventus*, equally in hard water: these are the species of general distribution.

Table 1. *Showing the occurrence of* Pisidium *in different kinds of habitats* (*Oldham*)

	Mountain lakes										
	Over 1000 ft.	Under 1000 ft.	Total	Lowland lakes and reservoirs	Rivers	Canals	Streams	Running drains, etc.	Ponds	Marshy places, ditches, trickles, etc.	Total
Number of loci	52	94	146	13	61	35	14	28	78	91	466
amnicum	0	0	0	3	39	23	1	1	0	0	67
cinereum	28	35	63	8	42	20	1	9	18	34	195
conventus	3	2	5	0	0	0	0	0	0	0	5
henslowanum	0	4	4	6	42	30	1	6	0	0	89
hibernicum	24	57	81	1	13	9	5	6	1	0	116
lilljeborgii	14	44	58	0	0	2	0	0	0	0	60
milium	10	27	37	7	17	9	3	15	23	10	121
nitidum	12	47	59	11	46	28	10	17	23	3	197
obtusale	7	11	18	2	0	0	0	3	26	25	74
personatum	2	7	9	3	4	3	1	1	7	50	78
pulchellum	0	7	7	2	8	5	2	13	1	0	38
subtruncatum	1	26	27	12	51	32	14	21	31	8	196
supinum	0	0	0	0	20	11	0	0	0	0	31
tenuilineatum	0	0	0	0	3	4	0	0	0	0	7
torquatum	0	0	0	0	9	14	0	0	0	0	23
Average number of species	1·9	2·8	2·5	4·2	4·8	5·4	2·7	3·3	1·7	1·4	2·8
Loci with only one species	26	28	54	0	0	0	2	6	41	60	163

Table 2. *Showing the concurrences of the species of* Pisidium *with one another* (*Oldham*)

	amnicum	*cinereum*	*conventus*	*henslowanum*	*hibernicum*	*lilljeborgii*	*milium*	*nitidum*	*obtusale*	*personatum*	*pulchellum*	*subtruncatum*	*supinum*	*tenuilineatum*	*torquatum*	Total
Alone	0	34	2	1	16	8	9	9	40	32	3	9	0	0	0	—
With other species	67	161	3	88	100	52	112	188	34	46	35	187	31	7	23	—
Total	67	195	5	89	116	60	121	197	74	78	38	196	31	7	23	—
amnicum	—	48	0	60	15	1	21	53	0	4	12	59	27	5	23	67
cinereum	48	—	1	59	40	26	46	93	16	38	9	95	29	6	21	195
conventus	0	1	—	0	1	3	0	1	1	0	0	0	0	0	0	5
henslowanum	60	59	0	—	20	5	25	72	0	5	17	76	29	6	23	89
hibernicum	15	40	1	20	—	36	46	66	16	8	15	52	3	1	2	116
lilljeborgii	1	26	3	5	36	—	15	31	7	1	5	17	0	0	0	60
milium	21	46	0	25	46	15	—	82	16	7	23	82	1	0	1	121
nitidum	53	93	1	72	66	31	82	—	10	13	29	146	23	6	20	197
obtusale	0	16	1	0	16	7	16	10	—	9	0	5	0	0	0	74
personatum	4	38	0	5	8	1	7	13	9	—	2	14	1	0	2	78
pulchellum	12	9	0	17	15	5	23	29	0	2	—	33	1	1	1	38
subtruncatum	59	95	0	76	52	17	82	146	5	14	33	—	25	7	23	196
supinum	27	29	0	29	3	0	1	23	0	1	1	25	—	6	18	31
tenuilineatum	5	6	0	6	1	0	0	6	0	0	1	7	6	—	6	7
torquatum	23	21	0	23	2	0	1	20	0	2	1	23	18	6	—	23
Average number of companions	4·7	2·7	1·4	4·5	2·7	2·4	3·0	3·3	1·1	1·3	3·9	3·2	5·3	6·3	6·1	

Table 3. *Showing the percentage concurrences of the species of* Pisidium *with one another, the total occurrences being taken as* 100 (*Oldham*)

	amnicum	*cinereum*	*henslowanum*	*hibernicum*	*lilljeborgii*	*milium*	*nitidum*	*obtusale*	*personatum*	*pulchellum*	*subtruncatum*	*supinum*	*torquatum*
Alone	0	17	1	14	13	7	5	54	41	8	5	0	0
With other species	100	83	99	86	87	93	95	46	59	92	95	100	100
Total	100	100	100	100	100	100	100	100	100	100	100	100	100
amnicum	—	25	67	13	2	17	27	0	5	32	30	87	100
cinereum	77	—	66	34	43	38	47	22	49	24	48	94	91
henslowanum	90	30	—	17	8	20	37	0	6	45	39	94	100
hibernicum	22	21	22	—	60	38	33	22	10	39	27	10	9
lilljeborgii	1	13	6	31	—	12	16	9	1	13	9	0	0
milium	31	24	28	40	25	—	42	22	9	61	42	3	4
nitidum	79	48	81	57	52	68	—	14	17	76	75	74	87
obtusale	0	8	0	14	12	13	5	—	12	0	3	0	0
personatum	6	20	6	7	2	6	7	11	—	5	7	3	9
pulchellum	18	5	19	13	8	19	15	0	3	—	17	3	4
subtruncatum	88	49	85	45	28	68	74	7	18	87	—	81	100
supinum	40	15	33	3	0	1	12	0	1	3	13	—	78
torquatum	34	11	26	2	0	1	10	0	3	3	12	58	—

Turning to the general character of the habitats, *amnicum, supinum, tenuilineatum* and *torquatum* are restricted to running water and so mostly are *henslowanum*, lowland *hibernicum* and *pulchellum*: *cinereum, milium, nitidum* and *subtruncatum* can live also in small closed ponds (as in the Aldenham ponds) and *obtusale* and *personatum* prefer such places, while *subtruncatum* and *nitidum* prefer running water: *conventus* and *lilljeborgii* have special habits. We may also construct a sort of hierarchy of gentility starting with *personatum*, which lives in the slums, through *obtusale, cinereum, milium, nitidum* and *subtruncatum*, *hibernicum* to *henslowanum* and *amnicum* which insist on the best places with 4 or 5 other species and *supinum, tenuilineatum* and *torquatum* which are even more particular. This is the same sort of series which I drew up for land snails without specialised habitats (**273**) and which may be made for most of our water snails though without such splendid data as Mr Oldham provides. The best indices of the position of any species are the frequency with which it occurs by itself and the number of other kinds which live with it, which is a measure of the general goodness of the locus: these are shown in Table 2. Thus *amnicum* "never" occurs by itself and is accompanied by *henslowanum, subtruncatum, nitidum* and *cinereum* in 90, 88, 79 and 77 % of its loci respectively. Contrariwise, *obtusale* is alone in 54 % of its loci and was never found with *amnicum, henslowanum, pulchellum, supinum, tenuilineatum* or *torquatum*. The curious thing is that *obtusale* and *personatum*, both common in bad places, are found together only in 11 or 12 % of their occurrences: *obtusale* occurs more often than *personatum* with *hibernicum* and *milium* and less often with *cinerum*, which suggests what is the fact, that it affects bad places with more water in them than those in which *personatum* is found. However, it would be tedious to set out at length the various conclusions and suggestions which anyone who cares to study the tables may make out for themselves.

Alkins' (**50**) intensive study of a small area in Staffs. shows *henslowanum, hibernicum, milium, nitidum* and *subtruncatum* in the remains of a canal and the ponds and streams connected with it (i.e. the good places) and *personatum* in the bad places (ditches and marshes): *cinereum* was found in good and bad alike except in the drying loci in which *personatum* occurred alone. Stelfox (**82**) notes a concurrence of *cinereum, obtusale* and *personatum* in peaty waters in Ireland, sometimes with *milium* but not *subtruncatum*.

In 163 of the 466 loci a species was found by itself, and it is of some interest to consider how these solitary occurrences are made up. All those of *personatum* (32 in number) are mean lowland loci: so are 39 of the 40 for *obtusale* (the other being a mountain tarn), but here "pond" is commoner than "ditch or swamp": of the 34 for *cinereum*, 18 are mountain tarns, the rest ponds, ditches, etc.; all the 16 for *hibernicum* are mountain lakes, and this is no doubt its primary habitat (it occurs in 60 % of *lilljeborgii* loci), and where it spreads to lowland loci it needs good places with several other species: montane places account for 2 each of the few solitary occurrences of *milium*, *nitidum* and *subtruncatum*. But in 65 % of Oldham's loci more than one species was present and in many 4, 5 or 6; the average is 2·8. The highest number actually recorded is 9: *amnicum*, *cinereum*, *henslowanum*, *hibernicum*, *milium*, *nitidum*, *subtruncatum*, *supinum* and *torquatum* in R. Ouse in Bedford, and there are only 2 others (*pulchellum*, *tenuilineatum*) which could reasonably be expected there: the same with *personatum* and *pulchellum vice supinum* and *torquatum* were found in R. Gade in Herts. But as appears to be the rule (above, p. 127) no one place has all the species it might, though the rivers and canals of the south of England come near it. Thus in Oldham's careful survey of 40 lochs in the far north (**78**) 11 species were found and 8 were fairly common: one place yielded 6 and four others 5, and the commonest species (*lilljeborgii*) was found only in 24.

Phillips and Stelfox (**83**) have published an account of *hibernicum* and its companions in 74 Irish loci: the following table gives the percentage occurrence of other species with it and shows as good correspondence with Oldham's data as can be expected:

	Phillips and Stelfox	Oldham
amnicum	5	13
cinereum	32	34
henslowanum	19	17
lilljeborgii	15	31
milium	54	40
nitidum	70	57
obtusale	18	14
pulchellum	7	13
subtruncatum	51	45

the average number of companions being the same in both series (2·7).

(*b*) *Operculates*

The 10 operculates live almost exclusively in running water; being gill breathers and unable to come to the surface and gulp in air as the pulmonates do, they presumably need water which is fairly well oxygenated and also free from particles which might choke their gills.

Paludina **vivipara* (Fig. 40) and ***contecta* (Fig. 41) both occur in England as far north as Yorks. in slow fair-sized (below, p. 163) rivers, canals and large draining ditches. Neither occurs naturally in stagnant water or closed ponds, though they will sometimes live, apparently permanently, in ponds into which they have been introduced (**84**), also in ornamental garden ponds (**23**), and they will breed in large aquaria (**15**). Roughly speaking their habits seem to be identical and the two are often found together, but there is presumably some difference in their requirements, for *vivipara* is decidedly more widespread (39 English and 3 Welsh counties) and commoner though in parts of East Anglia *contecta* (27 English counties) alone is found. In France, Germain (**77**, **205**) says that *contecta* has less liking for running water than *vivipara* and frequents marshes and ponds rather than rivers and streams, and J. F. Musham (MS.) draws the same distinction in Lincolnshire.

Bithinia **tentaculata* (Fig. 35) and ***leachii* (Fig. 42) form a similar pair. *B. leachii* lives in the south-east and midlands up to Yorks. with an outlier in Stirling (**101**) and in half a dozen Irish counties in slow rivers, backwaters, canals and ditches, "always" in good

loci with many other species. Adams (**89**) was naturally surprised to find it in a pond in Essex with *Ancylus lacustris*, *Physa hypnorum* and *Sphaerium lacustre*, and I have seen it in a pond at Polegate (**177**) and in marl pits in Kent. *Bithinia tentaculata*, while still requiring good conditions, is less particular and much commoner and is found throughout England up to Edinburgh and throughout Ireland. It will be found in (nearly) every place where *leachii* occurs and also under less favourable conditions in lakes, reservoirs, quicker rivers and quite small streams. It never occurs naturally in small closed stagnant ponds, and attempts which I made to colonise it in 13 of the best of the Aldenham ponds all failed except that I found a few specimens in one of them (a running pond) 10 years later. But it does sometimes occur in the larger closed loci which marl pits provide in Cheshire (**85**) and Kent. Welch (**86**) points out that the distributions of *leachii* and *Planorbis corneus* are very similar both in England and Ireland.

***Valvata macrostoma* (Fig. 55) lives in draining ditches in Hampshire, the Sussex marshes and East Anglia—rich places with a good fauna of which Oldham (**87**) gives this example from Suffolk:

Ancylus lacustris	*Planorbis contortus*	*Bithinia leachii*
Limnaea peregra	*Pl. fontanus*	*Valvata piscinalis*
L. palustris	*Segmentina nitida*	*V. cristata*
L. truncatula	*Physa fontinalis*	*V. macrostoma*
Planorbis corneus	*Paludina contecta*	*Sphaerium corneum*
Pl. complanatus	*Bithinia tentaculata*	*Pisidium milium*
Pl. vortex		

†*Valvata piscinalis* (Fig. 11) is common throughout Britain and Ireland in all kinds of running water—rivers to quite small brooks, canals, ditches and lakes, including a few low-lying mountain lakes (e.g. L. Scarmclate, Caithness and L. Mhor East, Inverness); it is sometimes extremely abundant in running ditches, and trout may get a stomachful. Taylor (**88**) has recorded it in one pond used as a rubbish dump and Long (**220**) in an engine cistern, but such habitats are quite exceptional and it does not live in closed ponds. †*V. cristata* (Fig. 12) requires the peculiar combination of plenty of mud and running water which it generally gets among a dense growth of plants such as *Sparganium* in slow streams, backwaters, ditches, lakes, etc. It occurs throughout Britain and Ireland and is probably commoner than it seems to be, for it is easy to overlook and is frequently found on caddis cases (**43**).

†*Paludestrina jenkinsi* (Fig. 13) was first differentiated and described from specimens from brackish water in the Thames estuary in 1889 (**90**), and at that time there was nothing known in fresh water with which it could possibly have been confused. It was not, however, a new creation, for it has been identified in holocene deposits in England and Ireland and had been collected in Lough Neagh about 1837 and at Gravesend in 1859 (**94**). It was first found away from the coast in 1893 when Daniel (**91**) took it in a canal at Dudley; in 1897 Hann (**92**) found it in a stream at Middlesbrough, and in 1899 Taylor (**93**) in a canal at Droylesden. It has since become one of our common fresh-water species and has now been recorded in the Census of the Conchological Society for 56 of the 68 divisions of England and Wales, for 9 Scottish counties including Orkney, and for a number of places in the north and south of Ireland.

It is a most determined colonist and has been caught in passage with *Pisidium cinereum* and *P. subtruncatum* in mud on the bill of a scaup duck shot at Perth (**203**). Its passage from salt to fresh water is no doubt helped by its viviparous habit which gets round the difficulty that marine eggs do not contain enough salts for the development of the embryo (Needham, **167**). It is also parthenogenetic (**95**) which gives it an advantage over its unisexual allies (*P. stagnalis*, *P. ventrosa*) which lay eggs: it is also free from the parasitic castration by trematode larvae which is common in these other species. There is also something exceptional in its nitrogenous metabolism, for in a long list of terrestrial marine

and fresh-water Mollusca examined by Needham (**96**) it is the only one which showed no uric acid. Experimentally fresh-water strains may easily be got to live and breed in sea water: Ellis (**97**) showed that the acclimatisation of *P. stagnalis* to fresh water was favoured by warmth.

Inland it lives in running waters, rivers, canals, brooks, ditches, *running* ponds, often in the meanest little trickles. In stagnant water and closed ponds it is very uncommon: the Hampstead bathing ponds (**98**) and a dew pond at 370 ft. on the downs near Eastbourne (Shrubsole, **177**) are the only certain instances I know, though suggestive cases are mentioned by others (**99**). In many of its loci it occurs in the greatest abundance, and the vegetation and mud may be black with it: Stelfox (**103**) and Welch in Ireland and Stubbs (**100**) in England remark on the destructive effect it has on the existing Mollusca when it invades a locality. Conversely it rather frequently disappears from a place in which it has been abundant. These extravagances are characteristic of a species which has not yet found its settled place in our fauna; what that eventually becomes will be interesting to see. According to Dean (**218**) carp have a passion for it while perch leave it alone.

Amnicola taylori (Fig. 60), which appears to be native and not as has been supposed an importation, was first found by F. Taylor in 1900 in the Manchester canals (**102**) where it still lives without having spread far, and recently in a timber dock at Grangemouth in Stirling by A. R. Waterston (**101**).

***Neritina fluviatilis* (Fig. 43) occurs in small and large rivers, especially in the rapid parts, river lakes and canals, sitting on stones, the masonry of bridges, etc., more rarely on the plants, throughout England from Somerset and Dorset to Westmorland and Yorks., and in the central parts of Ireland: it has not been found in Devon and Cornwall, Wales (except Glamorgan) or Scotland except for an outlying locus in Harray Loch in Orkney (which has hard water), where it has been known since the time of Edward Forbes. In Ireland Stelfox (**103**, p. 121) says "strictly calcicole", and Moquin-Tandon (**104**) the same for France (see below, p. 158).

(*c*) *Pulmonates*

Phylogenetically the pulmonates (*Ancylus, Limnaea, Planorbis, Physa*) are land Mollusca which have taken to an aquatic life. In consequence they can breathe air and all of them (except the limpets, *Ancylus*) do this more or less, especially in warm weather, when they are fond of coming to the top and crawling about on the surface film. Otherwise they separate air from the water into their pulmonary cavity for hydrostatic as well as respiratory purposes or absorb what oxygen they need from that dissolved in the water; this suffices in the winter and in deep cold water. Foul water encourages aerial respiration, and in a dirty deoxygenated pond, sealed with a thick mat of *Lemna*, frogbit, etc., they may be found crawling about on the surface of the vegetation. In *Planorbis* respiration is facilitated by the presence of haemoglobin which is present in considerable quantities (**249**) in the larger species (*corneus, complanatus, carinatus*) and less uniformly in the smallest (*nautileus*). Their ancestry is perhaps also reflected in their capacity to survive in dry air for surprisingly long times.

†*Ancylus fluviatilis* (Fig. 2), the fresh-water limpet, has been recorded for all the comital divisions of England, Wales and Scotland except there; in Ireland it is less universal but common enough. It normally lives on stones in quick-running water, hard or soft, not only in large and medium rivers but in small streams and tiny trickles and on wet rocks (**221, 247**), even at the edge of the sea (**227**), and in some mountain lakes to over 2000 ft. It needs a hard clean surface to sit on (which may be supplied by the shell of another snail or a mussel or the elytron of *Dytiscus*, on which it has been caught taking an aerial journey, occasionally by plants, as well as by stones) to which it fits snugly because the edge of the shell consists of periostracum only (**261**). In any one stream it is sharply restricted to those

places where the turbulence of the current is sufficient to keep the stones clean; hence it is generally found in a rippling place in a few inches of water, and none will be seen in quieter places close by where the flow allows silt and mud to coat the bottom. If a stone carrying it is moved from the ripples into a slow place of about equal depth perhaps a yard away, the limpets have all gone by the next day. Their oxygen requirements are, I believe, rather high, for they die easily in a corked tube on the way home, but though this probably helps to determine their absence from stagnant water it is not the factor which fixes their distribution in a small shallow stream where all the water is no doubt adequately aerated. Why they object so strongly to mud is not clear, but it presumably interferes with respiration. Sitting as they do, only a small part of their body is exposed to the water from which they have to get the oxygen they need, since they cannot come to the surface and take in air like the other pulmonates, and this part is the first to be covered with mud. If the necessary conditions of hard surfaces and absence of mud[1] are satisfied, quickly running water is not obligatory. Clean lakes will do, or, as Fysher (**184**) says, places in lakes where the wave wash keeps the stones clean: Moore (**105**) found it in a well and Heathcote (**106**) in a cement tank in the Isle of Man, and I have seen it in another in Hampshire. Oldham (**107**) and Schroeder (**196**) have shown that it can be bred in an aquarium without running water which I had failed to do. Its habit of living in very shallow water must be a protection from fishes.

Ancylus lacustris (Fig. 27), more a southern species, definitely prefers quiet and stagnant water, though it equally needs a firm surface to sit on which it commonly finds in the stiff leaves and stems of water plants such as water-lilies or *Sparganium* and on floating or submerged timber or the shells of other Mollusca. It is common in cattle ponds, lowland lakes, ditches and quiet rivers. Its typical habitat is quite different from that of *A. fluviatilis*. The same river may easily contain both, each in its respective niche, but they are occasionally found actually together in places such as slow rivers: I have twice so seen them on water-lily leaves in quietly flowing, moderately deep water, and collocations of the two species are mentioned by others (**108**). André (**261**) says that experimentally it lives well in badly oxygenated water which *fluviatilis* will not.

†*Limnaea peregra* (Fig. 3) occurs throughout Britain in all types of habitats in which Mollusca occur at all, in stagnant, still and running water, from brackish marshes to 2000 ft. and over. It is our commonest and most abundant fresh-water snail, and with the probable exception of *Pisidium cinereum* our commonest mollusc. It is, however, absent from many loci which contain other snails, and descriptions such as "in every stream and pond" which occur in some local lists are exaggerations: in 1915 there were in Aldenham 116 effectively separate watery loci which contained Mollusca of some sort and *peregra* was present in only 59. It lives well in many stony mountain lakes with no other Mollusca than *Pisidium* and occasionally *Ancylus fluviatilis*, and in the mountains of Ireland, Wales and Scotland it is by far the commonest water snail. In these situations it sometimes develops curious local races (*Limnaea* "*involuta*" in south-west Ireland and north-west Scotland (**260**), *L.* "*burnetti*" in L. Skene near Moffat) in which the spire is more or less sunk in the later whorls (**111**): some of these breed fairly true in artificial culture. All the British forms which I have examined have a sessile spermatheca and would be called *limosa* or *ovata* on the Continent (**51, 77**).

**Limnaea auricularia* (Fig. 28) is more southern and eastern and is normally restricted to roomy habitats—slow rivers, canals, lowland lakes, reservoirs and *large* ponds. It does not like quick-running water, and it is very uncommon in small ponds into which I have vainly tried to introduce it. Curiously enough it sometimes flourishes prodigiously in artificial garden ponds even in west Cornwall, outside its normal range, and fountains, and it

[1] Dr Pentelow tells me that in the upper Tees it lives on stones coated with the fine debris from stone crushing plants.

has been introduced into North America (**17**) which the much commoner and more catholic *peregra* has failed to reach. It is never found naturally without a good many other species. In Scotland, where it reaches as far as Elgin, frequently in Ireland and occasionally in England it does not achieve the full development of its shell but matures and breeds in a juvenile form known as var. *acuta* or *lagotis*. It breeds early and then dies off so that it may be impossible to get adult specimens after June. The anatomical distinction from *L. peregra* is now clear (**51, 77, 111**), and it appears (Taylor MS.) that our pioneer anatomist, C. Ashford, knew of the essential point—the long spermatheca duct—as long ago as 1885: it would have saved much trouble if he had published it.

Limnaea stagnalis* (Fig. 29) similarly has a preference for spacious habitats, though it is not so particular as *auricularia* and is not uncommon in cattle ponds and occurs sometimes in fairly swift rivers especially in the south-east of England. I have twice found it abundant in isolated dew ponds on the Wiltshire downs (as has Hurst (226**) and Shrubsole on the south downs), and thrice seen it appear in one of the Aldenham ponds, flourish for 2 or 3 years and then die out again without obvious cause. It may also breed long before it attains its full size, which as far as I know *peregra* and *auricularia* do not do in nature, though *palustris* does. Geographically it occurs throughout England except in the west, over most of Ireland and in a few places in the south of Scotland, where Forbes and Hanley (**254**) and Ritchie (**14**) say it has been introduced. Baillie's (**292**) attempt to colonise it in Sutherland apparently failed.

†*Limnaea palustris* (Fig. 4) has been recorded for all except 3 comital areas in Great Britain as far north as Perth and has been found up to Caithness: it is widely distributed in Ireland. It lives in quiet and stagnant water, on the one hand in rich loci with a number of other species and on the other in poor places such as marshes and drying ditches and plashy places with no companions (above, p. 132): in Ireland, Stelfox (**103**, p. 112) notes it in peaty places with *Pisidium cinereum* and *P. personatum* where other Mollusca cannot live. Considering its range of tolerance one would expect it to be commoner than it is.

Limnaea glabra (Fig. 56) has been already dealt with (above, p. 128).

Limnaea truncatula has obtained some economic notoriety and special study by being the ordinary host of the sheep fluke (*Fasciola hepatica*), a role sometimes taken by *L. peregra*. It lives mostly out of water, on the mud at the edge of rivers, streams and ditches: sometimes in damp grass in hollows in fields, and also in the slacks of sand dunes (e.g. at Braunton and Berrow), where it endures very hot dry conditions in the summer. In mountain districts it is generally common in small trickles of water, up to 3000 ft. in the Black Mountains, but it does not tolerate really acid peaty ground. It is only occasionally found living in permanent water, and in this paper I do not reckon it as a water species.

***Amphipeplea glutinosa* (Fig. 52) is one of our rarest species and some of the old records[1] are hardly reliable: the shell alone is hard to distinguish from some forms of *Limnaea peregra*. It was known to Montagu (**35**, p. 380 and Suppl. p. 139) from the ditches in the marshes at Deal where it still lives (**114**). It has also been found in the Thames valley near Reading and Oxford, in the Stroud Canal, Norfolk, north Lincoln and south-east Yorks.: in Ireland in the L. Neagh basin and in the central limestone plain from Dublin to the west. It lives chiefly in draining ditches and canals, also in slow rivers (**113**) and some shallow Irish lakes. It sits on stones and the mud rather than among the plants, though Ashford (**112**) found it on water-lily leaves as Montagu records. Its reputation for vagariously appearing and disappearing is probably due to the adults breeding early in the summer and then dying off so that only infants are present during the usual holiday season (**115**).

**Planorbis corneus* (Fig. 30) is essentially an English species, mainly south-eastern, extending to Northumberland and in the west to Exeter, Llangorse Lake in Brecon and the

[1] E.g. from Bala and Windermere in Jeffreys (**141**).

Shropshire Union Canal at Chirk: in Scotland it has been found in Lanark, and in Ireland it appears to be truly native in Dublin, Kildare and Queen's County. Outlying occurrences should be regarded with suspicion, for it is well known to aquarists and pisciculturists and is always liable to be introduced as it has been in Sligo, Northern Ireland and elsewhere (**116**): Standen doubts whether it is really indigenous in south Lancs., and Oldham has the same suspicion in Cheshire. Its natural transport is difficult (above, p. 125), and it is not found in closed cattle ponds though it lives in them well enough; in a wild state it affects slow rivers, good ditches, canals, lowland lakes and reservoirs. Webster (**237**) says it is very sensitive to injury and dies if its shell is cracked, but experiments which I have made indicate that it mends its shell as well as, for example, *Limnaea peregra* and *L. stagnalis*. **Planorbis complanatus* (Fig. 31) (*umbilicatus, marginatus, planorbis*) and **Pl. carinatus* Fig. 32) are a pair of closely allied species with almost identical geographical ranges over the whole of England, south Scotland and most of Ireland. Their habitats are similar to those of *Limnaea stagnalis*—slow rivers, canals, running ditches, lakes, also in small closed ponds and marshes. In Ireland (**103, 193**) *complanatus* rather affects small ponds and ditches, while *carinatus* is found more in rivers and lakes, and roughly speaking the same distinction holds in England though with many exceptions. Müller (**43**) said of *carinatus* "in lacubus ac fossis" and of *complanatus* "in paludosis".

**Planorbis vortex* (Fig. 33) and †*Pl. spirorbis* (*leucostoma*) (Fig. 8) are another pair which it is not always easy to tell apart. They can occur together in large loci (rivers, lakes, canals), but typically *vortex* is found in running water with plenty of plants, while *spirorbis* affects stagnant and drying ponds and ditches (above, p. 129): *vortex* is occasionally present in closed ponds. ***Pl. vorticulus* (Fig. 53) occurs in draining ditches and a moat in Sussex and Norfolk.

†*Planorbis albus* (Fig. 5) is more catholic in its tastes than *complanatus, carinatus* and *vortex*, and has a wider geographical range through the whole of England, Wales and Ireland and up to Sutherland in Scotland. It lives freely enough in good loci with *Limnaea auricularia, Planorbis corneus*, etc., but it can put up with much meaner places—small ponds, small weedy streams, rather quick rivers, marshes, and it has been found by Oldham at 1450 ft. in the Welsh hills with *Pisidium lilljeborgii* and by Gyngell (**164**) under stones in a fast moorland stream in Yorks. It or *Planorbis contortus* is the most likely *Planorbis* to be found by itself in inferior loci with permanent water.

†*Planorbis contortus* (Fig. 9) is much the same, ranging to Shetland. In my own experience I should associate it particularly with running water in good loci, but it occurs fairly often in stagnant pools, ditches and marshes and sometimes in mountain lakes: in Ireland (**103**) it is frequent in peaty drains with no companions except *Pisidium*. White (**129**) says it is the most abundant *Planorbis* in Scotland.

**Planorbis fontanus* (Fig. 34) is also widely distributed, but it is rather more particular where it lives though one would never be surprised to find it in any water, running or stagnant, which contained other snails. It is particularly common (commoner than *albus* or *contortus*) in closed ponds in the south of England.

†*Planorbis nautileus* (*crista*) (Fig. 7) is widespread in stagnant and running water throughout Britain: it is small and rather easily overlooked, and its frequency would be better appreciated if it were searched for more carefully; it is often easiest found by taking home a bag of weed and rubbish and washing it out in hot water as was recommended by Unwin (**117**; **247**, p. 218). This is probably the explanation of its frequent absence from lists of Mollusca from rich loci which contain nobler and more impressive species. But, making allowance for this, it seems to have no great preference for "good" over "bad" places (above, p. 132), and it certainly occurs in many of the latter though I think I was wrong (**7**, p. 179) in suggesting that it is secluded into undesirable homes by competition. Shrubsole (**177**) has found it in a dew pond in Sussex.

Of *Planorbis glaber* (*laevis*) (Fig. 6) I know nothing by personal experience except that it is possible to breed it in an aquarium in quite hard water. Records of it, especially from odd or unlikely places, need critical scrutiny, for it is easy to confuse it with immature *albus* in which the longitudinal striation is badly developed: *Valvata cristata* has also been mistaken for it, even by the elect. Reliable records seem to show that it is a wild species mostly north-western and living characteristically in shallow low-lying "mountain" lakes, generally near the sea, either among the weeds or on bare stones (**78**). In such places it is common on the west coast of Ireland (**103**) and has been found in a good many places in Scotland and the north of England. Of many of the southern records I am more doubtful, but Cooper (**180**) has had it lately in a draining ditch at Aldeburgh in Suffolk.

***Planorbis acronicus* (*stroemii*) (Fig. 57) is confined to the Thames and its tributaries, where it lives in quiet parts of the rivers and backwaters.

Planorbis dilatatus is an American species, first found (**73**, p. 221) in 1869 by Thomas Rogers in two places in canals near Manchester. It has since turned up in a variety of similar habitats in the district (**118**) and in the R. Tame with which the canals communicate (**119**). But it has not spread further than Burnley (20 miles), where it was known in 1886 though almost the whole of England is open to it via the canals. It probably prefers places where the water is warmed by engine effluents, but it is not restricted to them.

***Segmentina nitida* is a rare southern and eastern species, going as far north as Yorks. and with outlying stations in the Severn valley in Montgomery (**120**) and Glamorgan. It flourishes chiefly in marsh draining ditches as round Deal, in Sussex, Norfolk, Cambridge and Lincoln, and an example of its companions has been already given (above, p. 140). But it has also been found scattered about here and there in ponds, not apparently always very attractive ones, as in the lower Thames valley (**35**, **121**) and at Welshpool, Blackpool, Stourport and Highclere. In Yorkshire it lives in Askern Bog, Dringhouses (and Askham) Bog and Hornsea Mere and the neighbouring ponds (**122**): these places are relics of larger marshes, and it seems likely that its natural habitat is in marshes which used to be much more widespread than they are now (**123**) and occupied the valleys of the untamed rivers. If it occurs at all in rivers, streams and canals it is very uncommon.

†*Physa fontinalis* (Fig. 10) occurs all over England, Wales and Scotland, as far as Aberdeen, and generally in Ireland. It is characteristic of clean, bright, running water with plenty of plants in rivers, streams, running ditches and sometimes lakes (e.g. Windermere and L. Skene in Aberdeen, where Macgillivray (**124**) found it 92 years ago and A. R. Waterston last year). It is not particular about volume and so lives in quite small loci, as in a closed pond on blown sand in Co. Mayo (Oldham). It is "never" (see below, p. 166) found in closed ponds or stagnant water, but it will breed in a good-sized aquarium (Oldham).

Physa hypnorum (Fig. 59) has been considered above (p. 131).

Physa acuta (Fig. 58) is a polymorphous species scattered over Europe and the Near East which reaches its northern limit in this country where it occurs either in greenhouses (e.g. at Kew, Newcastle, Glasgow) or in engine tanks which may be always warm, e.g. at Aberdeen (**126**), or only sometimes, e.g. at Kettering, or in the open air as in the R. Brent at Golder's Green or the R. Tame at Ashton-under-Lyne (**119**) or the Manchester canals or the canal at Aylesbury (**125**). A few attempts which I made to colonise it from the Brent to cattle ponds met with no success. The idea that some of these occurrences represent the American *P. heterostropha* is not clearly justified.

4. The relevant qualities of habitats

As with land Mollusca, it is unsatisfying to make lists of the inhabitants of loci distinguished and described by their general nature and appearance without trying to determine the particular qualities of them which are im-

portant to the Mollusca. We need, if possible, to look at the world from the molluscs' point of view, and it is unlikely that their categories correspond with our own. "Woods", for example, do not form a significant category for land Mollusca, for we find that what they contain depends on their age and the soil they grow on rather than on their botanical constitution, and that "woodland" species occur in a number of places which are not woods at all in the ordinary sense of the term. In the same way water Mollusca do not look on "rivers" or "ponds" as one of the primary kinds of places which are available for them to live in: what matters to them is rate of flow, nature of bottom, quality of water, etc., and the Mollusca of one river may differ more from those of another river than from those of a lake or pond. In this section, therefore, I try to make out what it is in different habitats which snails really care about. As one would expect, the various factors are almost inextricably mixed with one another, and the final result is often the product of conflicting elements:

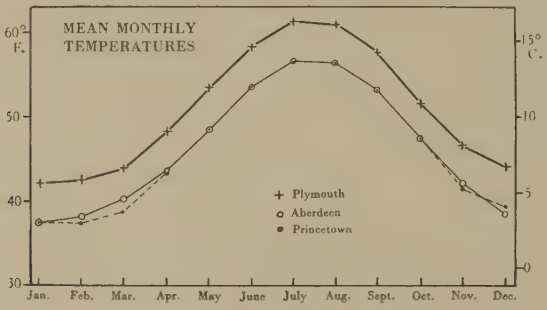


Fig. 1.

thus rate of flow may compensate for absence of sunshine, sunshine for indifferent water, lime for stagnation, and so on. With land Mollusca, the main factors are lime and shelter (which means dampness), and I think the following discussion may be summed up by saying that *the chief considerations for water Mollusca are lime and water which is clean in the sense of being transparent and not overcharged with the products of animal and vegetable decay:* it should at any rate be read with this conclusion in mind.

(*a*) *Altitude*

Browsing in the *Book of Normals* issued by the Meteorological Office (1919) I was surprised to find that the mean monthly temperatures at Princetown on Dartmoor were almost identical with those at Aberdeen (Fig. 1), the mean annual figures being 46·2 and 46·3° F. respectively. Princetown is 1243 ft. above Plymouth, 14 miles distant, where the annual mean is 51·0° F. These figures correspond well enough with the usual allowance (**274**) of 1° F. of mean temperature for each 300 ft. altitude and each 100 miles latitude. I know

of nothing but casual temperature records for high British mountain lakes and streams, and the data for air temperatures cannot be transferred to them without qualification. On the whole high lakes are probably colder than would correspond to the calculated air temperatures even when all the winter snow is gone, because water temperatures depend a great deal on direct sunshine which in mountains is defective owing to cloud and fog, and corrie lakes facing north lose much of what sunshine there is. Certainly such lakes as L. Coire an Lochain in the Cairngorms at 3267 ft. (the highest named loch in Britain[1] and free from Mollusca) can be uncomfortably cold to paddle in in August. Shallow lakes open to the sun may, however, warm up fairly well: West (**284**) notes up to 67° F. at 2200 ft. and (**282**, vol. I, p. 165) mentions 70° F. in "small hill lochs" in Scotland, perhaps because such temperatures struck him as exceptional. Without having any of the desirable details therefore it seems that a lake at 2000 ft. in North Wales or at 1000 ft. in Perthshire is, *quâ* temperature, somewhere north of Britain altogether.

Since practically all the ground over 1500 ft. is on the older, siliceous rocks, the water in high loci also differs from that in lower places by being soft and often very soft with the single exception of Malham Tarn at 1250 ft. in north-west Yorkshire, which is the only calcareous mountain lake in Britain and as will be seen (below, p. 157) an illuminating place. Bwch Llyn (p. 155) at 970 ft. in Radnor is also calcareous though not exactly a mountain lake.

The following list contains what I have been able to collect about the occurrence of our Mollusca at altitudes of 1000 ft. or thereby and over, the 7 species marked * occurring at these heights only in calcareous water:

Ancylus fluviatilis: 2300 ft. Brandon Mt., Kerry (**80**); 2000 ft. L. Cwm Clyd, north Wales; 1700 ft. L. Skene, Dumfries (**111**), etc.

**A. lacustris*: 970 ft. Bwch Llyn, Radnor (J. W. Vaughan).

Limnaea peregra: "2400 ft." Lochan a' Chait on Ben Lawers (**283**, 1895, p. 246); 2000 ft. Farragon, Perth (J. Leslie in **45**); 1750 ft. L. Glas in Cwm Clogwyn, north Wales (Oldham); 1600 ft. L. Einich, Inverness: *L. "burnetti"*, 1700 ft. L. Skene; *L. "involuta"*, 1600 ft. L. Toberavanaha, Cork (**111**), etc.

**L. stagnalis*: 1250 ft. Malham Tarn, Yorks.; 970 ft. Bwch Llyn.

L. glabra: 1100 ft. Stafford (**46**).

Planorbis albus: 1450 ft. L. y Garn, Merioneth (Oldham); 1100 ft. L. Hilyn, Radnor; 950 ft. L. Ordie, Perth (A. R. Waterston); up to 1000 ft. in Scotland (**129**).

**Pl. nautileus*: 1250 ft. Malham Tarn.

Pl. spirorbis: 1250 ft. marsh by Malham Tarn (Roebuck MS.); 1000 ft. Breidden Hill, Montgomery (J. B. Morgan).

Pl. contortus: 1600 ft. L. Skiach, Perth (A. R. Waterston); 1250 ft. Malham Tarn; 1046 ft. L. Morlich, Inverness (J. E. Somerville); 984 ft. L. Ogwen, N. Wales (Oldham).

**Pl. fontanus*: 970 ft. Bwch Llyn.

Physa fontinalis: 950 ft. L. Ordie (**130** and A. R. Waterston).

**Bithinia tentaculata*: 1250 ft. Malham Tarn; 970 ft. Bwch Llyn.

Valvata piscinalis: 1250 ft. Malham Tarn; 970 ft. Bwch Llyn; 950 ft. L. Ordie.

[1] So say the Geological Survey (**131**). But C. Plumb (*Walking in the Grampians*, 1935, p. 91) seems rightly to give the record to Lochan Buidhe at 3650 ft. 2½ miles to the east.

Sphaerium corneum: 1600 ft. Little L. Skiach, Perth (A. R. Waterston); 1250 ft. Malham Tarn; 1200 ft. L. Kinardochy, Perth.

Sph. lacustre: 1050 ft. Stafford (**225**).

**Pisidium amnicum*: 1250 ft. Malham Tarn.

And for the smaller *Pisidium*, the unlocalised lakes being in Snowdonia and the records mostly by Oldham, from whose register the number of additional loci over 1000 ft. are taken:

Pisidium cinereum: 2400 ft. Ffynnon Felen in Cwm Glas; 2300 ft. Cam Chreag, Perth (Waterston); 2250 ft. L. Glas in Cwm Glas; 2000 ft. Kelly's Loch, on Lug Naquillia, Wicklow, and 28 more over 1000 ft.

P. conventus: 2400 ft. Ffynnon Felen; 2300 Brandon Mt., Kerry (Stelfox, **80**); and 3 more.

P. hibernicum: 2300 ft. Brandon Mt.; 2000 ft. Kelly's Lough; and 24 more.

P. lilljeborgii: 2300 ft. Cam Chreag; 2250 ft. Lochan a' Chait, Perth (F. F. Laidlaw[1]); 2000 ft. Kelly's Lough; 2000 Llyn Lync y Caws; 2000 ft. Llyn Cwm Clyd; and 14 more.

P. milium: 2300 ft. Cam Chreag; 2250 ft. Ffynnon Loer; and 10 more.

P. nitidum: 1600 ft. L. Toberavanaha, Cork; 1450 ft. L. y Garn, Merioneth; and 10 more.

P. obtusale: 2300 ft. Cam Chreag; 2250 ft. Kelly's Lough; 1740 ft. Llyn Dulyn, Merioneth; and 6 more.

P. personatum: 3000 ft. Perth (W. Evans, **145**); 2700 ft. Brandon Mt., 2250 ft. Llyn Glas in Cwm Glas; and 2 more.

**P. pulchellum*: 970 ft. Bwch Llyn.

P. subtruncatum: 1560 ft. Angle Tarn, Patterdale; 1100 ft. Llyn Hilyn, Radnor.

(*b*) *Lime*

There can I think be no doubt that as with land Mollusca lime is favourable and that hard water is better than soft, but in the absence of more ample analytical data than we have it is rather difficult to demonstrate and assess its importance. The great trouble is to disentangle the quality of the water from (*a*) geographical distribution, with which indeed it is obviously connected, for in a general way our calcareous strata lie in the south-east and the soft-water districts in the west and north, and (*b*) the physical characters of the habitats, since in the calcareous areas the rivers are mostly slow and ponds abundant, while elsewhere we have rapid rivers and numerous springs and streams. Hence it is not easy to find habitats close together which differ in nothing else than the hardness or softness of the water, and I suspect that such convenient contrasts can hardly be expected, for hard water generally contains much more plant growth than soft water (see **229**, **284**), which inevitably produces a difference in shelter, humus, etc., which is significant for snails and other animals. We have, too, to bear in mind that the final effect of oecological factors is their sum and that, again as with land Mollusca, the beneficent influence of calcium may be overridden by other unfavourable circumstances, and more Mollusca may be found in a quiet soft-water lake than in a rough calcareous stream.

[1] This is the taking from which *P. lilljeborgii* was first recognised in this country by B. B. Woodward (**146**): picture of the lake by G. West on plate iv of vol. 1 of the *Bathymetrical Survey of Scottish Fresh-water Lochs* (1910).

To appreciate the influence of lime, we must realise that the snails' scale of "hardness" is not the same as our own. Domestically, water will not be called "hard" with less than about 50 mg. calcium per litre (=about 12 "degrees of hardness"), and will not be complained about with less than about 80 (=20 degrees). Correspondingly, water with 20 will be called "soft". In experience, 30 is perceptible in washing one's hands, and water in a hotel (which proved on analysis to have 33) once led me to finding some entirely unsuspected hard water in the neighbourhood. Similarly, while water at 20 is undoubtedly "soft" in the ordinary sense it is definitely inferior for shaving and bathing to water at 2. From the admittedly very imperfect data available it appears that there are a number of Mollusca which do not live in water with less than about 20 mg. calcium per litre, and water of this grade is "hard" to their way of thinking, while water of 40 or more seems "very hard". So, too, on the snail scale water is "soft" only if it has about 10 or less, and between 10 and 20 it might be called "rather soft", but any very detailed classification must obviously wait on further data. Other organisms calibrate the scale in a different way: thus Butcher (**229**), discussing the macrophytic vegetation of rivers, calls water with less than 8 "non-calcareous", with 8–40 "slightly calcareous", with 40–80 "moderately calcareous", and with over 80 "highly calcareous", and sanitarians (**148**) may call up to 60 "slightly hard". A completely graded series can be divided into sections only with reference to the application in hand, and some day we may be able to specify the range of hardness within which each species commonly lives.

In a large way the hardness of waters may be guessed a good deal more accurately from the geological map than the calcareousness of the surface soil (**132**, p. 9), since the water represents the deeper substance of the land rather than the superficial layers. But one meets with unexpected lime just as one does on land. Thus the old red sandstone of Herefordshire is calcareous on the surface only in small patches where cornstones crop out or there is calcareous glacial drift. But the few analyses of springs and streams which I have made myself all show hard water (78–134), and Richardson's ample data (**285**) indicate that all the underground waters of the area are hard. The same seems to be true of the old red sandstone in Caithness and Orkney, though the formation is not generally thought of as biologically calcareous. Similarly, I was shocked to find a roadside spring on the Devonian slates near Croyde in north Devon with 79. I have met with no instance of unexpected soft water. In a calcareous area, water which comes from underground seems to be harder than water collecting on the surface, and water standing in contact with highly calcareous ground may not dissolve very much: thus spring ponds on the very limy sand at Braunton Burrows gave 23 and 56, and a pond at Aldenham about half floored with lumps of chalk only 50. The nature of the calcareous strata also makes a difference: chalk is most soluble and gives water round 80–120 (above, p. 134), oolite is hardly less effective as seen in the upper parts of the Thames or in Dorset; but mountain limestone gives rise to less calcareous streams, e.g. R. Tees is 32, R. Lune and its components 29–55 (**133**), R. Tyne 35, the stream which comes out of the Mendips in Cheddar Gorge 55. Rivers which are geologically dubious are generally hard, though the Whitby Esk is only 6 while the geological map shows much oolite in its basin. Ponds in cultivated areas will generally be more or less calcareous owing to the lime which agriculture and human occupation bring with them, although their water

is for the most part rain water: 83 of the Aldenham closed ponds, which are in clay with flints or London clay overlying deep chalk, ranged from 16 to 85 with an average of 48. 3 were under 20 and 35 over 50. So, too, 14 closed cattle ponds in the red clay of Herefordshire were 28–101, average 61. For 13 dew ponds, some cemented, on the Sussex downs Martin (**134**) gives 11–121, average 43. Marl pits are always calcareous, since they were dug to get out calcareous boulder clay or some other form of lime. Even domestic rain water may collect a good deal of lime from asbestos tiles (**148**) or oolite slates. It is possible that the calcium content of surface ponds is raised by the rooted plants collecting salts from the soil and adding them to the water where they decay.

My figures are mostly from those which I have collected myself and from some kindly given me by Dr W. H. Pearsall: there are not nearly enough of them. The only substantial series of analyses that I know of are those of domestic supplies, actual or potential, made by E. Frankland and J. C. Morton, 60 years ago, for the River Pollution Commission (**135**), and the hardness figures in the official *Return as to water undertakings in England and Wales* (1915). Putting together all the data it seems that all the rivers—and by inference the rest of the waters too—of England are hard or rather hard (i.e. over 30) except in Cornwall, parts of Devon, most of Wales, the Lake District and the head waters of the streams which arise in the Pennines; in Scotland soft water is found in the south-west and in the northern half. The map of the distribution of *Limnaea stagnalis* (Fig. 29) represents pretty well the area in which hard water may be presumed. Really soft water comes mostly from uncultivated areas which is as it should be, since an adequate amount of lime is a prime necessity for any but the meanest agriculture. The soil in these areas, siliceous to begin with, remains undisturbed, the rainfall is generally high, and so the surface is thoroughly leached and the emergent water may be somewhere near distilled water. As follows from Pearsall's work on the evolution of lakes (**136**) the water tends to take more salts into solution and become harder as it goes further, so that the composition may vary a good deal at different points. Thus the R. Exe at Thorverton, 6 miles above Exeter, is 10 and no doubt above this softer still, but it soon afterwards receives the R. Creedy 29 and the R. Culm 51, so that the Exeter Ship Canal is 21–34: the Severn, in odd samples I have picked up, gave 5 at Llanidloes, 15 at Welshpool, 28 at Shrewsbury and 46 at Worcester.

There is no fresh-water species which is certainly calcifuge as *Zonitoides excavatus* is on land: *Limnaea glabra* may be (above, p. 129), and none of the few known loci for *Pisidium conventus* is calcareous. But all the other kinds have been found habitually frequently or occasionally in hard water, and it is easier to examine the matter by considering what species are known to occur fairly frequently in quite soft water (i.e. with calcium less than 5 or at any rate under 10). Most of our evidence comes from lakes which fortunately are more comparable among themselves than most other types of habitat. Of the snails, *Limnaea peregra* is by far the commonest: from south-west Ireland we have 8 instances in water of calcium 1 or less (**111**), from north Wales in less than 1, 1, 2, 5 and 8, from Scotland 20 instances under 5, the lowest being under 1. *Ancylus fluviatilis* is the next most common: from Kerry we have it in water of 1 and 2, from Wales in 2, 3 and 4, from Scotland in 2, 3, 4 and 4: both these species have also been found frequently in lakes and streams which are presumably soft but for which we have no analyses. Of the bivalves, *Unio margaritifer* is common (above, p. 133), and in *Pisidium, cinereum, hibernicum, lilljeborgii* and *nitidum,* which are known from a number of soft

waters, the lowest calcium being 3, less than 1, 1 and 1 respectively: *milium* and *subtruncatum* are less frequent but have been found in water as soft as 1 and 3. The other species are not common: *Planorbis contortus* is in L. Ogwen in north Wales and in L. Morlich, Inverness, both with calcium under 1; *Pl. albus* in L. Gareg-wen in Carnarvon with 7; *Ancylus fluviatilis, Limnaea peregra, Planorbis contortus, Pl. albus* and *Valvata piscinalis* in L. Lubnaig, Perth (**283**, 1895) with calcium 3; *V. piscinalis* in L. Assynt in 6; *Sphaerium corneum* in L. Padarn, north Wales, at 2 and in L. Kinardochy, Perth, at 8; *Pisidium conventus* from Cwm Glas, Snowdon, at 2 and *P. obtusale* from Cork at under 1. And for a number of occurrences in montane lakes we have no analytical evidence.

Under more generally favourable conditions, about 10 more may be added to this list of 15 species. Windermere (calcium 6–8, Pearsall; Butcher (**229**) gives $3\frac{1}{2}$), which is an exceptionally good soft-water lake, 128 ft. above sea-level, $5\frac{1}{2}$ square miles, mature, sheltered with plenty of plants, silt and mud and varied subhabitats in different parts, has 17 species (**137**, **164**):

Ancylus fluviatilis	*Planorbis contortus*	*Sphaerium lacustre*
A. lacustris	*Pl. spirorbis*	*Pisidium hibernicum*
Limnaea peregra	*Physa fontinalis*	*P. lilljeborgii*
L. palustris	*Valvata piscinalis*	*P. personatum*
Planorbis albus	*V. cristata*	*P. pulchellum*
Pl. nautileus	*Sphaerium corneum*	

In the same neighbourhood Farrer (**138**) records *Ancylus lacustris* from Bassenthwaite (calcium 7) and *Planorbis spirorbis* and *Valvata cristata* from Derwentwater (calcium 6) and Cockerell (**275**) *Limnaea peregra, Physa fontinalis* and *Valvata piscinalis* from Conistone Lake (calcium 5). Most soft-water lakes are at high altitudes or latitudes and deficient in plants and humus, but another particularly productive one is L. Leane at Killarney at 66 ft., 9 square miles, with calcium 7–11 in different samples where we found (**111**, **139**) 17 species, 13 of which are in Windermere:

Ancylus fluviatilis	*Planorbis contortus*	*Sphaerium corneum*
Limnaea peregra	*Physa fontinalis*	*Pisidium cinereum*
L. palustris	*Valvata piscinalis*	*P. hibernicum*
Planorbis albus	*V. cristata*	*P. lilljeborgii*
Pl. nautileus	*Paludestrina jenkinsi*	*P. nitidum*
Pl. spirorbis	*Unio margaritifer*	

This list of 26 species—those in the Windermere and Leane lists *plus Limnaea glabra, Pisidium conventus, P. milium, P. obtusale* and *P. subtruncatum*—includes all those which we can find in soft water without surprise and one—*Ancylus lacustris*—which I think ought not to be in the list. *Limnaea glabra* and *Pisidium conventus* have not been found in hard water and *Unio margaritifer* and *Pisidium lilljeborgii* are much more frequent in soft, but apart from these four they all live in, for example, R. Thames with calcium 80 or more and prefer hard water to soft. *Unio margaritifer* (above, p. 134) and *Pisidium lilljeborgii* (above, p. 136) have been taken in hard water often enough to show that it is not wholly repugnant to them. The various races of

2 *Ancylus fluviatilis* 3 *Limnaea peregra* 4 *Limnaea palustris* 5 *Planorbis albus* 6 *Planorbis glaber*

7 *Planorbis nautileus* 8 *Planorbis spirorbis* 9 *Planorbis contortus* 10 *Physa fontinalis* 11 *Valvata piscinalis*

12 *Valvata cristata* 13 *Paludestrina jenkinsi* 14 *Unio margaritifer* 15 *Sphaerium corneum* 16 *Sphaerium lacustre*

17 *Pisidium cinereum* 18 *Pisidium conventus* 19 *Pisidium hibernicum* 20 *Pisidium lilljeborgii* 21 *Pisidium milium*

22 *Pisidium nitidum* 23 *Pisidium obtusale* 24 *Pisidium personatum* 25 *Pisidium pulchellum* 26 *Pisidium subtruncatum*

SOFT-WATER SPECIES

Figs. 2—26.

27 *Ancylus lacustris* 28 *Limnaea auricularia* 29 *Limnaea stagnalis* 30 *Planorbis corneus* 31 *Planorbis complanatus*

32 *Planorbis carinatus* 33 *Planorbis vortex* 34 *Planorbis fontanus* 35 *Bithinia tentaculata* 36 *Anodonta cygnea*

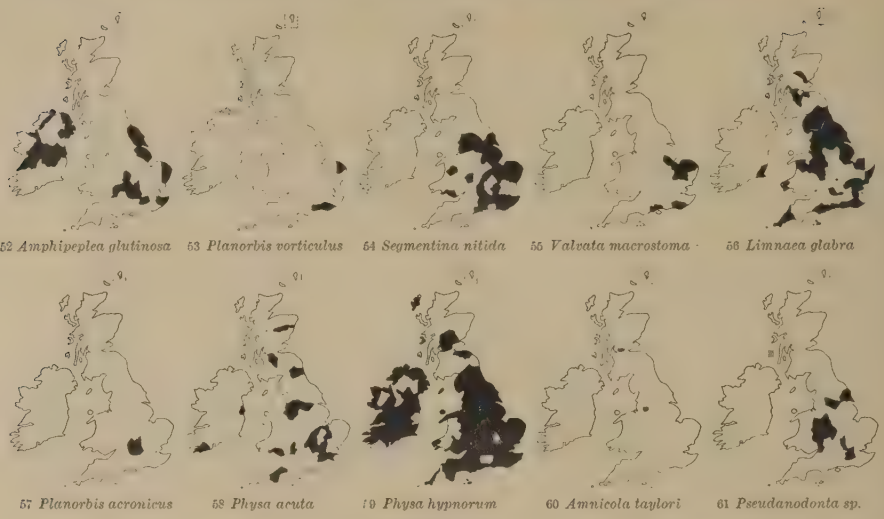
37 *Anodonta anatina* 38 *Pisidium amnicum* 39 *Pisidium henslowanum* 40 *Paludina vivipara* 41 *Paludina contecta*

42 *Bithinia leachii* 43 *Neritina fluviatilis* 44 *Dreissena polymorpha* 45 *Unio pictorum* 46 *Unio tumidus*

47 *Sphaerium rivicola* 48 *Sphaerium pallidum* 49 *Pisidium torquatum* 50 *Pisidium supinum* 51 *Pisidium tenuilineatum*

CALCIPHILE and CALCICOLE

Figs. 27—51.



Figs. 52—61.

Limnaea peregra from very soft water bear transplantation to water of 60 or 80 with complete equanimity.

Like the corresponding land snails which can do with very little lime (**132**, p. 34), these soft-water species are mostly small and widely spread in Britain (Figs. 2–26); many extend to northern Europe and some are holarctic: 21 of them have been found at 1000 ft. or over (above, p. 147).

Of the remaining species, for 6 (*Planorbis glaber*, *Pl. dilatatus*, *Physa acuta*, *Ph. hypnorum*, *Amnicola taylori* and *Dreissena polymorpha*) I have no adequate data on which to base any conclusion about their relation to lime: they can all live in hard water and none has been proved to occur in soft. *The other* 30 *are all calciphile or calcicole in the sense that they are habitually found in hard water*, and there is evidence that ordinarily they need water with at least 20 mg. calcium per litre and some of them more:

Ancylus lacustris	*Planorbis fontanus*	*Unio pictorum*
Limnaea auricularia	*Segmentina nitida*	*U. tumidus*
L. stagnalis	*Bithinia tentaculata*	*Pseudanodonta* sp.
Amphipeplea glutinosa	*B. leachii*	*Sphaerium rivicola*
Planorbis corneus	*Valvata macrostoma*	*S. ovale*
Pl. complanatus	*Paludina contecta*	*Pisidium amnicum*
Pl. carinatus	*P. vivipara*	*P. henslowanum*
Pl. acronicus	*Neritina fluviatilis*	*P. supinum*
Pl. vortex	*Anodonta cygnea*	*P. tenuilineatum*
Pl. vorticulus	*A. anatina*	*P. torquatum*

These are all more or less southern or south-eastern in range (Figs. 27–51) and are unknown or rare in Devon and Cornwall, Wales, the Lake District and most of Scotland. A number of them have large and heavy shells. Their

distributions either roughly correspond to, or are included within, the area in which practically all the water is hard and the coincidence is certainly suggestive. The best evidence that it is not fortuitous comes from a study of the periphery of the occupied areas towards the north and west, where soft water begins to be common; of the north I have no details and can give some data only about Wales and the south-west, where the outlying loci of various species prove to be calcareous.

Llyn Maelog, in Anglesea, is an outlying locality for *Limnaea auricularia*, *L. stagnalis* and *Anodonta*. It is a good-sized (about 800 × 400 yd.) shallow lake in the old sand-hills at Rhos Neigr with rocks at one end, a stony or sandy bed and sparse vegetation, including *Lobelia dortmanna* and *Subularia* as well as *Elodea*[1] and a reed bed on the western side. I am much indebted to Dr N. Woodhead of Bangor for much information about the persistent alkalinity of the water (*p*H 7·3–8·6): three samples gave calcium 17, 21 and 23, due no doubt to the calcareous sea sand, for the geology of that part of the island makes no suggestion of hard water. The conspicuous Mollusca have been known for 50 years (**140**, **142**), and the whole list is now:

Ancylus fluviatilis
Limnaea peregra
**L. auricularia acuta*
**L. stagnalis*
L. palustris
Planorbis albus
Pl. nautileus
Planorbis contortus
Physa fontinalis
Paludestrina jenkinsi
Valvata piscinalis
**Anodonta anatina*
Sphaerium corneum
Pisidium cinereum
Pisidium hibernicum
P. lilljeborgii
P. milium
P. nitidum
P. pulchellum
P. subtruncatum

* Calciphile.

L. Coron, 4 miles to the east, is practically a replica with calcium 23: it contains the same species *minus Limnaea palustris*, *Planorbis nautileus*, *Pl. contortus*, *Ancylus fluviatilis* and *Pisidium hibernicum* and *plus Ancylus lacustris*, **Anodonta cygnea* and **Pisidium henslowanum*.

There is no good local control for these lakes. The low-lying lakes round Snowdon are of a different type, stony river lakes with soft water[2] and no snails beyond *Limnaea peregra*, *Ancylus fluviatilis*, *Spherium corneum* and various *Pisidium*. But near Portmadoc, 25 miles away, there is the small L. Gareg-wen which, like Maelog, is embedded in the old sand hills against the rock. It has a sandy floor and abundant reeds, water-lilies, *Potamogeton perfoliatus*, *Myriophyllum*, *Littorella*, etc., and I have often wondered why it contained only *Limnaea peregra*, *Planorbis albus*, *Pisidium milium*, *P. nitidum* and *P. subtruncatum* until I examined the water and found the calcium only 7.

Bwch Llyn (sometimes called Llynbychllyn Pool) in Radnor, 6 miles south-east of Builth, is another significant locus discovered conchologically by J. W. Vaughan in 1905 (Roebuck MS.). About 700 × 250 yd., it lies in enclosed grassland at about 970 ft. on Silurian rocks which are not obviously calcareous:

[1] *Elodea* is very uncommon in soft water: on the other hand *Lobelia* is characteristic of soft water (**284**).

[2] L. Padarn calcium 2, L. Gwynant 4, L. y Ddinas 3, L. Quellyn 3.

there is a large reed bed, in parts a carpet of *Littorella* and much *Menyanthes*, water-lilies and *Potamogeton "lucens"*: three samples of water each gave calcium 21. The Mollusca are:

Ancylus lacustris
Limnaea peregra
**Limnaea stagnalis* (up to 52 mm. long)
Planorbis albus
Pl. contortus
**Planorbis fontanus*
Physa fontinalis
**Bithinia tentaculata*
Valvata piscinalis
Sphaerium corneum
Pisidium nitidum
P. personatum
P. pulchellum
P. subtruncatum

L. Gwyn[1], 14 miles away near Rhayader, is very similarly situated in a hollow of the hills at about 700 ft. on older Silurian strata. There is hardly any vegetation except *Littorella*. no snails and the calcium was 2: the contrast with Bwch Llyn is impressive.

Llangorse Lake (Llyn Safaddan), over which I had much help from Dr Betenson, on the old red sandstone near Brecon is another place which few would suspect of having hard water unless they saw it or the list of Mollusca (**143**) found in it: altitude 502 ft., about $1\frac{1}{4} \times \frac{1}{2}$ miles = 353 acres; abundant reed beds and aquatic vegetation with muddy or sandy floor, in parts with *Littorella* carpet. Two samples gave calcium 36 and 37, the effluent R. Llynfi 33 and its inflow 58 (in drought): the lime must come from neighbouring cornstones. The Mollusca are:

Ancylus lacustris
Limnaea peregra
**L. auricularia*
**L. stagnalis*
L. palustris
**Planorbis corneus*
**Pl. complanatus*
Pl. "glaber"
Pl. nautileus
Planorbis spirorbis
Pl. contortus
Pl. fontanus
Physa fontinalis
**Bithinia tentaculata*
Valvata piscinalis
V. cristata
**Anodonta cygnea*
**Unio pictorum*
Sphaerium corneum
**Pisidium amnicum*
**P. henslowanum*
P. milium
P. nitidum
P. pulchellum
P. subtruncatum

The profusion of Mollusca is extraordinary, and fishing from the landing stage among the *Potamogeton natans*, *Elodea* and *Lemna trisulca* reminds one of a first-rate calcareous locus in the south-east of England. In the effluent, *Limnaea stagnalis* and *Planorbis corneus* (which appeared in the lake between 1904 and 1928) were in such numbers as I do not think I have ever seen, and many *corneus* were as much as 33 mm. in diameter: *Bithinia tentaculata* reached 15 mm.

L. Maelog and L. Coron are the most westerly[2] loci for *Limnaea stagnalis*, and they are about 60 miles to the north and west of its nearest known habitat. Outside Glamorgan and Pembroke, in which there is a good deal of limestone, Wales is in general a soft-water area, and in this the species is known only from the four loci I have detailed with calcium 20, 23, 21 and 36, from a pond near Wrexham (Shrubsole, **65**) with calcium 28 and from one near Welshpool of which I know nothing further. In Herefordshire, next to the east and well to the west of the calcareous area of south-east England, it occurred in three

[1] The picture in the *Cambridge County Geography* of Radnor, p. 33, is not L. Gwyn, as it is labelled, or Bwch Llyn.

[2] Except for a rather dubious record from near Tenby based on a single young specimen.

places for which I have analyses—R. Lug with 58 and two running ponds with 70 and 88. L. Maelog and Bwch Llyn are softer than most of its homes, and now that it is known that these outlying Welsh lakes are calcareous most places where it is found can, I think, be presumed to have hard water. The position in England and Wales seems to be much the same as in Ireland where, Stelfox (**103**, p. 111) says, it is "widely distributed but seldom abundant outside the limestone areas of the central and eastern counties and absent from such peat-covered districts as west Cork, Kerry, north-west Mayo and north-west Donegal....It reaches the west coast in the sand dune" [and presumably calcareous] "lakes of west Mayo but does not live on any of the western islands". Shrubsole's (**65**) specimens from Wrexham were badly eroded, as he thought from the water being too soft, and Crowther (**276**) records the pertinent observation that he brought some into an aquarium at Leeds (where the tap water about 1929 had calcium 12), where they gnawed off the tops of one another's shells. Adult and young specimens from R. Colne (calcium 100) died in 2 days in R. Teign water (calcium 4).

Another place which brings out the favourable effect of lime on *Limnaea stagnalis* and others is Malham Tarn (plate 4) near Settle in Yorks., 153 acres at 1250 ft., up to 14 ft. deep, a wild stony lake with no marginal and little submerged vegetation (which, however, includes *Potamogeton lucens*, *praelongus* and *perfoliatus* (**258**)), many crayfish: Frankland (**135**) in 1869 gives the calcium as 54, Burrell (**149**) in 1899 found 32, and in 1935 we got 31, the lake lying on Silurian rocks at their junction with mountain limestone. The Wests (**286**) found plenty of desmids and nothing special in the phytoplankton, and do not seem to have known that the water was calcareous. The place has been frequently examined by members of the Yorkshire Naturalists' Union (**150**), and the Mollusca are:

Ancylus fluviatilis	*Planorbis contortus*	**Pisidium amnicum*
**Limnaea stagnalis*	*Physa fontinalis*	*P. cinereum*
L. peregra	**Bithinia tentaculata*	*P. hibernicum*
L. palustris	*Valvata piscinalis*	*P. lilljeborgii*
Planorbis albus	*Sphaerium corneum*	*P. nitidum*
Pl. nautileus		

Limnaea stagnalis, *Planorbis nautileus*, *Bithinia tentaculata* and *Pisidium amnicum* are unknown elsewhere at more than 1000 ft., and the fauna of Bwch Llyn (p. 155) at 970 ft. gives similar evidence of the encouraging influence of lime on *Ancylus lacustris* and *Planorbis fontanus*. No other loci for *Limnaea stagnalis* approach these altitudes and I know of no other place at 1000 ft. or over with anything like their faunas: most of the high lakes in north Wales and many of those in Ireland and Scotland have been examined conchologically.

The argument for the other species of this group is much the same and it need not be set out in detail. Towards the south-west, just where the soft-water area begins, *Limnaea auricularia*, *Planorbis corneus*, *Paludina vivipara* and *Sphaerium rivicola*, all species of characteristic calcicole distribution and

habit, have their last home in the Exeter Ship Canal and canalised river which, in a sample kindly obtained for me by Dr R. J. Lythgoe, showed calcium 34 and in a later specimen 21. Another western locus for *Paludina vivipara* in the Brecon and Newport Canal at Talybont gave calcium 27; the species, dreadfully eroded, lives here in profusion with *Bithinia tentaculata*, *Anadonta cygnea*, *A. anatina*, *Pisidium amnicum* and *P. henslowanum*, as it has been known to do for 62 years. For the Wye in Herefordshire I have a number of analyses varying from 15 to 33, and from the data given by Duncan and Ellis in Richardson (**285**) it appears that in times of drought the calcium may be a good deal higher: it contains *Bithinia tentaculata*, *Anodonta anatina*, *Unio pictorum*, *Pisidium amnicum*, *P. henslowanum*, *Neritina fluviatilis*, *Unio tumidus*, *Pisidium supinum* and *P. torquatum*, and going west from Hereford the conchologist will see little of any of them and nothing of the last four before he reaches the Irish Sea. The only Herefordshire habitat for *Planorbis corneus* was a running ditch with calcium 85, though it lived there for some years in a garden tank with about 20, as it did in Laver's water butt (above, p. 125). Shrubsole (**65**) put specimens from the Trent Canal (calcium 58) into Chester water (calcium 21) and found that they did badly and became deeply eroded.

The few calcareous loci known among the overwhelming majority of soft-water lakes and rivers in the northern half of Scotland also provide significant evidence, for it is in this hard water that the few calciphile southern species which spread so far north have been found. There are three highly calcareous lakes in the isle of Lismore, one of which is known to have water of calcium 60, (**282**) visited by Scott (**283**) and Standen and Hardy (**287**); five more on the Durness limestone in Sutherland investigated by Oldham with water from 20 to 32; about 8 on the old red sandstone in the north-east of Caithness where, Dr George Dick tells me, all the wells yield hard water, where Crampton (**288**) describes the flora of limy lakes and L. Watten has calcium 104 (Dr J. F. Tocher) and Yarehouse Loch 31; and perhaps half a dozen more in Orkney, where there is much lime in the old red sandstone and in the blown calcareous sand (**289**), all the deep and surface spring waters are very hard (Dr W. B. Bannerman) and Harray Loch[1] has calcium 78. In all, therefore, we know of about 20 calcareous lochs in the north, and they have been looked at conchologically (by Baillie, Scott, Oldham and others) more thoroughly than might have been expected. Four of the five southern calciphiles which have been found in the far north have occurred in these calcareous loci and are unknown or rare in the rest of Scotland; *Neritina fluviatilis* in Harray Loch in Orkney and *Planorbis vortex* in L. Hempriggs; *Anodonta anatina* in the River of Wick and *Pisidium henslowanum* in L. of Mey in Caithness. Of L. Achnacloich in Ross East where Scott (**283**) found *Planorbis fontanus* I know nothing relevant, nor of Hellier's Loch in Shetland where also Oldham got

[1] From Mr Robert Rendall.

Pisidium henslowanum: but it is not very rash to predict that when their waters are examined they will be found to be hard. But the molluscan fauna as a whole is poor, and apart from the five species mentioned the whole of Ross, Sutherland, Caithness, Orkney and Shetland[1] have only:

Ancylus fluviatilis	*Physa hypnorum*	*Pisidium hibernicum*
Limnaea peregra	*Paludestrina jenkinsi*	*P. lilljeborgii*
L. palustris	*Valvata piscinalis*	*P. milium*
Planorbis albus	*V. cristata*	*P. nitidum*
Pl. glaber	*Unio margaritifer*	*P. obtusale*
Pl. nautileus	*Sphaerium corneum*	*P. personatum*
Pl. spirorbis	*Sph. lacustre*	*P. pulchellum*
Pl. contortus	*Pisidium cinereum*	*P. subtruncatum*

and the Lismore lakes have 7 from this list.

It is quite clear that the absence of conspicuous southern calciphiles such as *Limnaea stagnalis*, *L. auricularia*, *Planorbis corneus*, *Pl. complanatus*, *Ancylus lacustris* and *Bithinia tentaculata* is not due to the absence of hard water. The calcareous lakes too are richer than the others; in a direct comparison in Sutherland Oldham got an average of 6·8 species per lake for the former against 2·7 for the latter, and it seems that, as with some of the land snails, some of the soft-water species become calciphile in the north.

Such is, as I believe, the general truth about the relationships of the various species to hard and soft water and geographical distribution, and it will commonly hold good, at any rate in England, Wales and the south of Scotland. Also apparently in Ireland where the calcareous area is central and north-eastern. As Stelfox (**103**, **152**) describes it, such species as *Ancylus lacustris*, *Limnaea stagnalis*, *Amphipeplea glutinosa*, *Planorbis complanatus*, *Pl. carinatus*, *Pl. vortex*, *Neritina fluviatilis*, *Anodonta cygnea* and *Pisidium amnicum* are central; *Planorbis albus*, *Pl. fontanus*, *Bithinia tentaculata* and *Sphaerium corneum* are mainly central, and though they occur in the generally non-calcareous districts of the south-west and north they are rare; while *Ancylus fluviatilis*, *Limnaea peregra*, *L. palustris*, *Planorbis nautileus*, *Pl. spirorbis*, *Pl. contortus*, etc., are ubiquitous. He attributes the absence of what I should call the calcicole species from the periphery to the difficulty they have had in crossing mountain ranges from the central plain. So, too, any critic who did not much believe in the importance of lime might take the maps on pp. 152–4 as illustrations of the varying capacity of the different species to spread through Britain from the south-east as the glacial period faded away.

And just as indifferent species may find a good supply of lime necessary or pleasant in the extreme north, so, under exceptionally good general conditions, calcicole species may live in quite soft water. The north-western branches of the Shropshire Union Canal are filled with water above Llangollen from the R. Dee, a typical turbulent mountain river with calcium 4 or 5. At

[1] Scott (**283**) examined 55 lochs in Shetland and found *Limnaea peregra* in 13, *Planorbis albus* 1, *Pl. glaber* 1, *Pl. nautileus* 9, *Pl. contortus* 1, and *Pisidium* 10.

the Chain Bridge such water as is necessary passes into a quiet, gently flowing stream in the canal, free from floods and any great fluctuations of level, moderately supplied with plants, including *Elodea* and frogbit, and now practically undisturbed by traffic: various samples taken in 1934 and 1935 showed calcium figures of 5–8 over the first 10 miles. In 1935 Oldham and I found the following 12 calcicoles:

Limnaea auricularia	*Planorbis vortex*	*Pisidium amnicum*
L. stagnalis	*Pl. fontanus*	*P. henslowanum*
Planorbis corneus	*Bithinia tentaculata*	*P. tenuilineatum*
Pl. carinatus	*Sphaerium pallidum*	*P. torquatum*

most of which Oldham had taken in 1922 when he found also *Bithinia leachii* which is in the ordinary way addicted to highly calcareous water. There were in addition 15 indifferent species. Further south near Welshpool, where the water has taken up more lime and has calcium 11–13, we found also

Paludina vivipara	*Unio pictorum*	*Sphaerium rivicola*
Anodonta anatina		

and here *Unio termidus* was found by Morgan (**290**) years ago. This locus is of course artificial, and to it snails have access through continuous water from the whole of the Midlands as well as very acceptable conditions when they get there. It is of particular interest because it flatly breaks the rules for about 15 species, none of which are known elsewhere from water with less than calcium 20 at least; it does not show that the rules are not sound but that one oecological factor must be balanced against another. The canal is perhaps analogous to an aquarium, and what happens when one tries to breed calcicole species in soft water no one seems to know.

The decided preference which most Mollusca have for hard water is due to several causes. (*a*) They need lime for their shells, and the calcicole species have on the whole larger and heavier shells than those which are content with soft water. This is not, however, a universal difference: on the one hand *Amphipeplea glutinosa* confined to quite hard water has a thin shell, while *Unio margaritifer* grows very heavy shells in quite soft water, though some which Oldham got from the Burn of Setter in Shetland had so little substance that the contraction of the periostracum on drying cracked the shells across, while specimens from the Hereford Wye, which has more calcium than most of its habitats, are small and rather thin (**257**). Bloomer (**178**) notes that the thickness of *Anodonta* is not always related to the hardness and softness of the water. *Limnaea peregra* from very soft water nearly always have thin shells (weighing 2 or 3 mg.) which may be so little calcified as to be flexible when they are fresh as in *L.* "*praetenuis*", though *L.* "*burnetti*" is an exceptionally large heavy form (135 mg.) and comes from water with calcium only 4. The thin-shelled races which I have bred in hard water have invariably responded by thickening the shell, so that cleaning out the body ceases to be the hazardous procedure it is with the soft water original (**111**). (*b*) The second great function which lime plays for snails is to agglutinate

Photo. Harmer, Settle

Phot. 2. Malham Tarn, north-west Yorkshire. The only calcareous lake in Britain over 1000 ft., calcium 39 mg. per litre; 1250 ft. above sea level; open and exposed, the highest ground near being only 1800 ft. Mollusca: 16 species (see p. 157).

Photo. Frith, Reigate

Phot. 3. Cwm Glas on Snowdon, Carnarvonshire. Illustrating about the extreme austerity which mollusca tolerate in Britain. In the larger lake behind (Ffynnon Frech; 2250 ft.; calcium 2) are *Ancylus fluviatilis* and *Pisidium personatum*: the smaller one in front (Ffynnon Felen; 2400 ft.; calcium 2) contains *Pisidium conventus* and, at a trickle entering it, *P. cinereum*. The distant lakes are L. Cwm y Ffynnon (1254 ft.) above Penygwrhyd and L. Mymbyr (588 ft.) at Capel Curig.

and precipitate particles of clay and so produce clear, bright water which will let in the sunlight: permanently and densely muddy waters contain hardly any plants and no Mollusca except sometimes *Anodonta*. The bad effect can be readily demonstrated by making an aquarium persistently muddy with clay, when after a few weeks the plants and snails wilt away. Particles, too, must be objectionable to the gill-breathing operculates. Quite soft natural water is generally clear enough, for it is found in places where there is little or no clay, and it may remain clear even in heavy floods: very hard chalk streams are also brilliantly clear because the clay is precipitated. Cloudiness is generally seen in moderately hard water and where the particular clay is resistant to agglutination. Different clays vary widely in this respect (**7**) and I have analysed a permanently very muddy pond at calcium 55. (*c*) A good supply of soluble salts, of which calcium itself may not be the most important, is desirable for the growth of most water plants, and the vegetation of hard water is always richer than of a corresponding habitat with soft water (**195**, **229**). West (in **282**) says that "peaty" water inhibits the natural decay of vegetable debris and that in it the plants are remarkably free from epiphytic organisms. (*d*) Calcium in river water also helps estuarine animals to bear the alternations between fresh and salt water (**206**).

(*c*) *Reaction*

It would be unconventional beyond the bounds of propriety to make no mention of hydrogen-ion concentration. Broadly speaking, for the natural waters of this country the reactions run parallel with the quantities of calcium, and *p*H determinations have the advantage over calcium measurements that they can easily be done at once on the spot, whereas calcium estimations need laboratory facilities or an amiable collaborator. A bottle of the "universal indicator" of British Drug Houses is indeed as useful in the field as one of acid for soil testing, but though it is a good servant it is, I think, a bad master, and I have been dissatisfied and rather bewildered by the results I have obtained. Frankly acid peaty water of *p*H 6 or less contains no snails as Carpenter (**153**) points out, and *Limnaea peregra* soon dies in water of 5·6; I have not come across any such water except in peat, and it should be noted that water stained brown from peat is not necessarily acid; it may have a *p*H of 7–7·5 (**229**), hence "peaty water" can be ambiguous. Ordinary soft mountain water is commonly about 6·5–7 and contains some Mollusca, though the calcium may be less than 1, and as the alkalinity increases we find more and more snails till we reach the highest figure of about 8·5 found in this country in which the calcium will normally be of the order of 60 or more and Mollusca abundant. It is the difficulty of being precise between 6·5 and 8·5 which is disappointing: this is due to the preponderating influence of the CO_2. Is one to take the *p*H of the water as it stands or after bringing it into equilibrium with air as Atkins (**233**) and others have done? Many acid waters become

alkaline when they are so treated, and the change is much more in some waters than in others. Thus a hard-water spring with calcium 134 may at its source be colorimetrically identical with a softish river (calcium 17) into which it falls, and Saunders (**202**) found that spring water of *p*H 7·2 soon rose to 8·2–8·5 as it flowed along and might reach 9 with much vegetation and sunshine. The effect of green plants and illumination is indeed disconcerting if one wants to attach a particular figure to a particular water. The late F. M. Turner showed me that a jar with *Elodea* may start at 6·5 in the morning and be alkaline to phenolphthalein before the end of a sunny day—a hundredfold decrease in hydrogen ions: corresponding changes occur in tanks and ponds (**200**), and different parts of the same pond may give different results: the diurnal change is perceptible even in rapid rivers (**154**) where the proportion of plants to water is quite small. Atkins and Harris (**169**) record variations from 7·6 to 9·3 and 6·0 to 8·0 in the same habitat at different seasons, and Welch (**278**) gives other examples in his interesting book on the conditions of life in fresh waters which has appeared too recently for me to refer to it as fully as it deserves. It is then hard to see how the *p*H of any water is to be specified, and it is impossible to make a scale relating it to the calcium content which seems to be the more important factor. If a definitive stable constant is wanted for any water the only thing to do seems to be to take its *p*H in equilibrium with air which may fail to express the actual existing conditions. The method therefore has considerable limitations, though no one would of course dispute its usefulness in quickly distinguishing acid and alkaline water in the field.

The oscillations in reaction which have been mentioned should theoretically be accompanied by changes in the calcium content in the sense that as the water becomes more alkaline from loss of CO_2 calcium carbonate should be precipitated. I do not know whether this has actually been quantitatively verified in nature, but the decalcifying effect of vegetation and sunlight would in effect make little difference to the snails for whom the calcium would still be available on the floor or, more conveniently, on the leaves of the plants mixed with the epiphytic Algae of which they are so fond.

The hardness in its turn does not remain constant, but the variations are proportionately much less than those of the *p*H. Thus in weekly trials over a year the Thames at Pangbourne varied from calcium 88 to 113, the Kennet from 82 to 108 and the Enborne, a much smaller stream, from 45 (in a flood) to 95 (**252**), and 134 samples in 12 months from the same point in the Thames varied from 68 to 140 (**148**). Butcher (**235**) found the R. Wharfe between 32 and 48 at monthly examinations over 2 years, and I have had figures from 15 to 33 for the R. Wye at Hereford, depending on what proportion of the water is coming from the Welsh moors.

Gammarus pulex is a familiar indicator of loci which are good for snails: Atkins (**212**) says that it dies in water less alkaline than 7·4, and though it often occurs in soft water it is much more abundant in hard.

(*d*) *Size and volume*

The larger units of water are liable to contain the more Mollusca if only because the chances of importation have been greater and they contain a greater variety of subhabitats—a consideration which applies particularly to *Pisidium*. There are, too, a number of species, mostly big ones, which show a great preference for and are almost restricted to what may be called large loci, i.e. good-sized rivers, canals, large draining ditches, lakes and large ponds (by which I mean ponds of about $\frac{1}{4}$ acre area and upwards, the depth being perhaps as important as the area). Among these are:

Limnaea auricularia	*Unio pictorum*	*Anodonta anatina*
Bithinia leachii	*U. tumidus*	*Pseudanodonta* sp.
Paludina contecta	*U. margaritifer*	*Sphaerium rivicola*
P. vivipara	*Anodonta cygnea*	*Pisidium supinum*
Neritina fluviatilis		

For the large mussels the explanation may be that the fish on which they are dependent need roomy places; for *Paludina* that they want deep water into which they may retire for the winter (**22**). Other species:

Limnaea stagnalis	*Planorbis complanatus*	*Bithinia tentaculata*
Planorbis corneus	*Pl. carinatus*	

show the same habit but less markedly, and all of them are found from time to time in small (e.g. surface 200 sq. yd.) ponds or (*Bithinia*) in small streams.

The failure of a number of these species to reach the upper, smaller parts of the rivers in which they live may be due to this size question or to the generally more rapid currents, but whatever the explanation the rich fauna of a river such as the Thames fades away progressively as one goes up its branches without there being any very conspicuous change in the obvious physical characters. Montagu (**35**, p. 387) notices the phenomenon for *Paludina* in the Kennet, Kendall, Dean and Rankin (**155**, p. 359) for *Neritina* in Lonsdale, French (**156**) for the same and "other species" in Essex. It is true for *Paludina* and *Neritina* in the Hertfordshire Colne, in the Lea and the upper branches of the Thames; for *Bithinia tentaculata* in the Herefordshire Wye. No species, except perhaps *Limnaea glabra* and *Pisidium personatum*, show any disinclination to live in large habitats as such, and we have none in this country which are particularly attached to springs and small streams as, for example, *Bythinella* is in Europe.

In lakes and large rivers of normal contours and in large deep ponds such as clay pits, the area occupied by molluscs is only a small part of the whole, and the proportion of animals and plants to water is much less than in a shallow pond. In the depths there may be some *Pisidium* though we know little of the Mollusca which live in water more than 6 or 8 ft. deep: *Anodonta* and *Unio* commonly live in shallower water, and when the emptying of a pool or lake allows a comprehensive view they are limited to a defined depth zone of 2–4 ft. (**28**, p. 96; **157**), though in a reservoir with steep sides they may have to live in 15–20 ft. *Sphaerium*, most *Pisidium* and the gastropods all

live their active lives in quite shallow water—an inch to 2 ft. or thereabouts—and so occupy only a narrow zone[1] round the edge of a large locus where most of the plants also grow. If there are plants such as *Potamogeton lucens* or water-lilies which root in deeper water, some of the pulmonates may be found among them, but beyond the greatest plant depth (which is largely determined by the transparency of the water (**136**, **158**)) there will be none. The effective occupied volume is therefore in contact with a larger, often much larger, volume of what may be called "free" water, and this is of some importance in promoting cleanness and diluting the products of activity and decay. Large loci of good depth are in this way equivalent to running water to which all the 13 species in the list on p. 163 are addicted: *Gammarus* has analogous habits, occurring as it does in lakes, *large* ponds and running water and not in the small ponds where *Asellus* flourishes.

Lists for several large lakes have been already given (pp. 151, 156) and the best follows (p. 172). The largest I know for closed ponds are both from Cheshire. Milne and Oldham (**84**) record

Limnaea peregra
L. auricularia
L. stagnalis
Planorbis corneus
Pl. complanatus
Planorbis albus
Pl. vortex
Paludina contecta
Bithinia tentaculata
Anodonta cygnea
Anodonta anatina
Sphaerium corneum
Sph. lacustre
Pisidium spp.

the *L. stagnalis* and *P. contecta* having been introduced. Britten and Williams (**85**) found in about a third of an acre:

Limnaea peregra
L. palustris
Planorbis albus
Pl. nautileus
Planorbis vortex
Physa fontinalis
Bithinia tentaculata
Valvata cristata
Anodonta cygnea
Sphaerium corneum
Pisidium spp.

These closed ponds are large enough to carry some species (*Limnaea auricularia*, *Planorbis vortex*, *Physa fontinalis*, *Bithinia tentaculata*, *Anodonta*) commonly associated with running water, and in comparison I give the list, for which I am indebted to Dr J. W. Jackson, of a larger habitat of a peculiar local type in the same neighbourhood with a stream running through it—Rostherne Mere, 118 acres, calcium 27 (**279**):

Ancylus fluviatilis
A. lacustris
Limnaea peregra
L. auricularia
Planorbis carinatus
Pl. albus
Pl. vortex
Pl. contortus
Pl. fontanus
Paludestrina jenkinsi
Bithinia tentaculata
Valvata piscinalis
V. cristata
Anodonta cygnea
Sphaerium corneum
Sph. lacustre
Pisidium cinereum
Pisidium henslowanum
P. hibernicum
P. milium
P. nitidum
P. obtusale
P. personatum
P. pulchellum
P. subtruncatum

[1] The importance of this marginal zone is predominant. Ponds with vertical sides make poor habitats as do many reservoirs. In streams and reservoirs in which the water level fluctuates violently this zone is disturbed and disorganised and snails thoroughly dislike such places. Fresh rain water also seems to be disagreeable and few Mollusca can be found in loci flooded up with it, perhaps because it contains too little trihydrol (**210**); if so, water from melting snow or ice ought to be favourable.

At the other end of the scale, we know that quite small loci may contain many snails though their average content is small (above, p. 127). Among the Aldenham closed cattle ponds we have one which at its fullest (seldom reached) measures 17 × 9 yd. with about 3 ft. of water at the deepest which contains

Ancylus lacustris	*Planorbis fontanus*	*Pisidium milium*
Limnaea peregra	*Sphaerium corneum*	*P. personatum*
Planorbis nautileus	*Sph. lacustre*	

and another 9 yd. across with about 18 in. of water with

Limnaea stagnalis	*Planorbis nautileus*	*Sphaerium lacustre*
Planorbis complanatus	*Pl. fontanus*	*Pisidium milium*

To both of these *Planorbis corneus* was added without any deterioration of the existing faunas which have remained constant for about 18 years. Other species which can be comfortable in these restricted loci are

Limnaea palustris	*Planorbis contortus*	*Pisidium obtusale*
Planorbis albus	*Pisidium cinereum*	*P. subtruncatum*
Pl. vortex	*P. nitidum*	

making some 18 species for which such places are adequate. Loci of standing water which are smaller than this are commonly not permanent and dry up in the summer: here we have (above, p. 128):

Limnaea peregra	*Planorbis spirorbis*	*Pisidium cinereum*
L. palustris	*Pl. nautileus*	*P. obtusale*
L. glabra	*Physa hypnorum*	*P. personatum*

The tiniest loci are necessarily running water and are provided by springs and trickles with miniature rapids and pools and with perhaps nowhere more than a couple of inches of water. *Pisidium cinereum* and *P. personatum* are the commonest inhabitants and in some places frequent: *Limnaea peregra*, *L. palustris* and *Paludestrina jenkinsi* can also survive, and also *Ancylus fluviatilis*.

(*e*) *Still and running water*

About two-thirds of our species evidently prefer and are generally found in water which is more or less running, but, as far as I can see, none is inseparably attached to running water *per se*. The most familiar species which one associates with quick streams and rivers are *Unio margaritifer* and the limpet *Ancylus fluviatilis*, and the latter is plainly adapted to live in currents. But the pressure of running water is unnecessary, for both of them flourish in clean river lakes in which the current is hardly perceptible. What they both need is clean water free from silt and mud, and this is usually attained by a rapid flow; if, however, it is achieved otherwise, a flow can be dispensed with. The same principle lies behind the general superiority of gently running over quite stagnant water: slow rivers, canals and marsh drains are among our richest habitats, and a cattle pond with a trickle of water through it shows

more species than a similar closed pond—in the Aldenham series an average of 9 against one of 3·7, the best (21 × 15 yd.) giving 13:

Ancylus lacustris	*Planorbis vortex*	*Pisidium milium*
Limneae peregra	*Pl. contortus*	*P. obtusale*
L. palustris	*Pl. fontanus*	*P. personatum*
Planorbis albus	*Paludestrina jenkinsi*	*P. subtruncatum*
Pl. nautileus		

Movement mixes up the water and secures better oxygenation, it washes away the debris of plants and the products of their decomposition and prevents the excessive overgrowth of slimy algae (which snails do not like). Some closed ponds form satisfactory self-contained units which go on indefinitely like a balanced aquarium: others are choked with decaying vegetation and the decay may be putrefactive, the water is foul and there are no snails.[1] Long's (**220**) extraordinary record for an engine cistern at Burnley—*Limnaea peregra*, *Planorbis corneus*, *Pl. albus*, *Pl. dilatatus*, *Pl. fontanus*, *Bithinia tentaculata*, *Valvata piscinalis*, *Sphaerium corneum* and *Sph. lacustre*—must in part at least be due to the constant renewal of the water.

Water which runs too fast is relatively sterile. There is no mud and, it may be, not even sand for plants to root in, and what there is is constantly being disturbed. No Mollusca except the larger bivalves, adult *Dreissena* and *Ancylus* can avoid being swept away by the current and in floods even these will be killed by the moving stones. Hence violent streams generally contain no molluscs and indeed little life of any kind unless there are quiet corners of retreat. All rivers and streams are in fact largely dominated by their current as regards the vegetation (**229**) in which the pulmonates mostly live, and when it dies down in the winter (as much of it does) they lose its protection though in its summer heyday it helps them by keeping the water quieter. Hence pulmonates and especially *Planorbis* are more affected than the operculates and bivalves which live on the bottom, though *Sphaerium* and *Pisidium* are related to the plants as agents for gathering mud and silt. Fox and Simmonds (**293**) show that *Asellus* from running water uses more oxygen than from quiet water, which may have something to do with the poverty of fast streams.

Considering the species individually, there are a certain number which any collector would associate with water which is running fast enough to ripple in shallow places and to stream out the plants:

Ancylus fluviatilis	*Paludestrina jenkinsi*	*Unio margaritifer*
Limnaea peregra	*Neritina fluviatilis*	*Pisidium amnicum*
Physa fontinalis		

[1] The flow through closed ponds has no gross cleaning effect. Rain water comes in, and passes out largely by percolation through the sides and floor. Since the average annual rainfall in south England exceeds the loss by evaporation by about 10 in. and the ponds keep somewhere about the same level, the amount passing through is not inconsiderable, but it carries nothing particulate away with it though it tends to prevent the concentration of dissolved substances becoming excessive.

But the list is indeterminate because "running water" is a vague term, and it will be more precise to catalogue those which frequently live in stagnant water such as is found in closed ponds:

Ancylus lacustris	*Planorbis complanatus*	*Pisidium cinereum*
Limnaea peregra	*Pl. spirorbis*	*P. milium*
L. palustris	*Pl. contortus*	*P. nitidum*
L. stagnalis	*Pl. fontanus*	*P. obtusale*
L. glabra	*Physa hypnorum*	*P. personatum*
Planorbis albus	*Sphaerium corneum*	*P. subtruncatum*
Pl. nautileus	*Sph. lacustre*	

and to realise that all the other species prefer and are mostly restricted to water which is in some degree moving. As has been suggested, a slow flow may be imitated by increasing the proportion of unoccupied or "free" water, hence large, deep, stagnant loci may contain running water species. Some deep marl pits near Sissinghurst in Kent used to contain (**242**) *Bithinia tentaculata*, *B. leachii*, *Anodonta cygnea* and *Unio pictorum*, and *Bithinia tentaculata* lives in similar pits near Manchester (**84**, **85**). *Limnaea auricularia*, *Planorbis corneus* and *Paludina vivipara* live well in garden fountains which are flushed and kept clean.

Of the 20 in the stagnant list, all (except possibly *Limnaea glabra*, *Physa hypnorum*, *Pisidium personatum* and *P. obtusale* (above, p. 128)) are equally content with gently running water and several of them prefer it. Hence "running" water (which I should interpret as clean oxygenated water) is more favourable than stagnant water so long as it does not run too violently: which corresponds with common experience.

(*f*) *Sunlight and pollution*

In clean running water some Mollusca can live in the dark and have been found in water mains (e.g. **238**), though whether they breed in such situations is less certain. But as Huggins (**159**) and Crowther (**168**) have noted, snails enjoy sunshine and are more active in it both in aquaria and in the field, and their response is so immediate that it must be to the light rather than the warmth. Carnally more important, however, is the indirect effect through the plants, great and small. Adequate light means green plants to oxygenate the water and coating Algae for the snails to eat. Through the oxygenation it also ensures that the decomposition of plant and animal remains, which is a necessary part of the water cycle, shall take a bland course without gross foulness or putrefaction which uses up the oxygen in the water and produces poisonous substances. I do not pretend to understand the detailed differences between aerobic and anaerobic (putrefactive) decomposition, but I know that foul water is generally snailless, that when an aquarium jar "goes wrong" and smells the snails will die although they can get plenty of oxygen at the surface and that ponds with stinking black mud do not generally yield any bivalves though the water above may be clean and fruitful.

In thick muddy water into which sunlight cannot penetrate there is little animal or vegetable life and in consequence little decomposition; it fails as a molluscan habitat in a negative way. The positive harmfulness of poisonous substances is added in densely shaded ponds and streams which have few or no plants and are littered with a trash of twigs and leaves. Leaves are bad, especially perhaps oak leaves, though I have found *Planorbis nautileus* and *Sphaerium lacustre* in ponds floored with them. Woody tissue seems to be worse; I have never found anything in ponds in woods,[1] and field ponds sufficiently shaded with trees or bushes to depress the vegetation are usually poor places. The same result is seen when the water is shaded with a thick growth of reeds (*Typha*, *Phragmites*, *Phalaris* etc.) or, towards the end of the summer only, with a mat of *Lemna*. Sunlight, in short, prevents what may be called natural pollution.

Artificial pollution acts in the same way. Effluents from sewage works, beet factories, metalliferous mines and various industrial processes contain either putrescible material or poisonous substances which kill the plants or animals or both. The devastating effects are familiar to conchologists in the north of England (**160**) and have lately been described in detail for a beet factory (**53**) and for lead and zinc mines in Wales by Carpenter (**161**). The pollution may be only temporary, and sterilised streams are repopulated from uncontaminated branches. A small amount of organic (sewage) contamination may actually increase the Mollusca by encouraging plants and improving the humus, and water snails are strikingly immune to the effects of smoke which is so injurious to land Mollusca (**187**, **223**) as the rich fauna of the Manchester canals shows (below, p. 175).

(*g*) *Temperature*

Generally speaking, our Mollusca are active, grow and breed only in the summer, and within the range of our climate the hotter it is the better. We have no cold rivers fed from permanent snow fields, and the cool upland head streams which have interesting relations with some planarians (**162**, **163**) would have no more Mollusca if they were warm. Nor are we much concerned with large deep lakes such as L. Ness or L. Morar or L. Tay, in which the surface temperature does not rise above 60° F. in the summer or fall below about 42° F. in the winter (Wedderburn in **282**); James Murray and Scott (**283**) remark that they are very poor in Mollusca. The loci in which most of our snails live are so small that their temperatures quickly follow the air temperatures and sunshine and so mean that few data have been collected. Wesenberg-Lund (**282**) emphasises the importance of shallow water and sunshine, and Pearsall (**291**) gives useful data and points out that the water is over 50° F. (10° C.) and over 59° F. (15° C.) for 5 and 2 months respectively in the large Cumberland lakes and for 7 and 5 months in neighbouring ponds.

[1] Mr Oldham tells me that *Pisidium obtusale* sometimes occurs in such places.

The papers of Guppy (**170**) are an illuminating example of what a sensible naturalist can do with a thermometer. He points out, for instance, that what matters to snails and many other small fresh-water animals and to the plants is the temperature in the very shallow weedy water at the edge of the pond or river; most of them live in this zone, and the water readily heats up in sunshine till it is a good deal hotter than the air, and being entangled in vegetation it is not much cooled by mixture. Ponds round Kingston are at the surface 6–12° F. (3–7° C.) warmer than the neighbouring Thames, and the shallow marginal water may reach 80 or 85° F. (27 or 29° C.) on a hot summer afternoon; it has, too, a daily range of as much as 20° F. (11° C.) and the Thames only 1 or 2° F. My own observations, as far as they go, fully bear this out, and a hot sunny day often raises the temperature of the snails' immediate surroundings to 30° C. or thereabouts. In a pond crowded with vegetation there is little mixing and there may be marked stratification, e.g. 65° F.

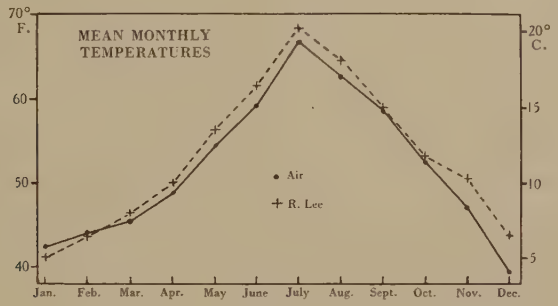


Fig. 62.

(18° C.) at bottom 4 ft. deep, 75° F. (24° C.) at surface and 85° F. (29° C.) at edge. With open water, with wind action and still more with running water the whole is at much the same temperature which tends to be higher the smaller the volume. On the whole the temperatures of lowland waters are rather higher than the corresponding air temperatures, especially during the night.

A continuous temperature of 30° C. is probably more than our species could tolerate: warm greenhouses are certainly bad places for breeding aquaria which do much better out of doors than inside a house: there is indeed experimental evidence (**171**) that brief spells of daily cooling promote the breeding of *Limnaea stagnalis*. In aquarium jars a temperature of 104 or 113° F. (40 or 45° C.) for several hours or repeated on successive days is needed to kill *L. peregra* or *Planorbis nautileus*, the eggs being rather more delicate. Such figures are occasionally reached in hot sunny weather, but the natural habitats never approach this fatal heat.

Correspondingly, cold such as we experience does no perceptible harm[1] except perhaps by killing the susceptible *Elodea*, and like other fresh-water animals snails can be frozen into ice for a good time without being killed (**172**). There is no resting phase: the animals mostly pass the winter about half-grown, never as eggs. They hibernate in the mud or deeper water and are difficult to find, though a hardy species such as *Limnaea peregra* or *Planorbis corneus* may sometimes be seen crawling about under ice and I have noticed *Pl. spirorbis* quite active in water at 1° C. In mild spells in the winter *Limnaea peregra* can make considerable growth

It is natural to suppose that the cooler climate is responsible for the failure of so many southern species to live in the northern two-thirds of Scotland, but it is difficult to be sure about it. The soft-water districts in Cornwall, west Wales and the Lake District are not much richer in species for all their blander climates, and some of the southern species (e.g. *Limnaea stagnalis*, *Planorbis corneus*, *Bithinia tentaculata*) in Scandinavia and Siberia live through far more severe winters than we have anywhere, though a hot summer is perhaps more important than a relatively warm winter. From their altitudes, Malham Tarn (p. 157) and Bwch Llyn (p. 155) should be climatically equivalent to Orkney and Fort William. Hence one might not unreasonably suppose that a suitably calcareous lake in the north of Scotland would have a rich fauna just as the maritime calcicoles on land (e.g. *Helix itala*, *H. barbara*) spread right up the west coast to Cape Wrath. We now know, however, that this is not so (above, p. 159), and rejecting the chemical and suspecting the climatic explanation we may contemplate the possibility that the southern species have, with few exceptions, not yet had time and opportunity to get so far. The nearness of suitable habitats to one another is an important factor in the dispersal of water snails, and for a species needing calcareous water the journey through Scotland is difficult, for such places are few and far between.

(*h*) *Vegetation*

Most of the germane points about plants have been incidentally mentioned already. We may note also these:

(1) While a good supply of submerged vegetation is in every way favourable, too thick a growth is harmful. This is best seen with *Elodea*, and a pond overfull, or, as one says, "choked" with it, will not produce many snails, or if it has several species none of them will be abundant. The same is true of aquaria which may easily have too much weed. The injurious effect of the filamentous Algae known as "blanket" or "flannel" weed (**209**) may be analogous. Both impede free movement, and the Algae often attach themselves to the apex of the shells with the result that the snails are "absalomed".

(2) A free growth of plants is an important factor in providing the humus

[1] The altogether exceptional winter of 1933–4 in which the ponds were frozen when they were more or less empty seems to have had a devastating effect on the plants and snails.

which helps so much to make the bottom of a field pond watertight and the locus permanent and offers a safe refuge for the Mollusca if the place goes dry in an exceptional summer: drying does no damage so long as the bottom is soft and pulpy even if it is not perceptibly damp (**9**); ponds which dry every year have no chance to grow plants and accumulate humus, they dry hard and the results are disastrous to any but the few species which can tolerate the conditions (above, p. 128). On the other hand emergent marginal plants (*Alisma*, *Sparganium*, etc.) collect earth and mud at their roots and largely help in converting water into dry land, first at the edge and then by their progressive invasion over the whole, so that in the end the locus is destroyed.

(3) These emergent plants are also effective in drying up small loci, and their transpiration puts the finishing touch to the effects of a hot dry summer. Ponds without these hold water longer under severe conditions, and in the summer of 1934 a cement tank in my garden with three good clumps of *Alisma plantago* lost 19 in. of water, while a precisely similar tank 6 ft. away with *Potamogeton crispus* and *Lemna* lost only 5 in. The roots of plants are also said to perforate the puddle of dew ponds and make them leak (Shrubsole).

5. The Mollusca of different habitats

Apart from a few rare species of quite limited distribution (*Planorbis vorticulus*, *Pl. acronicus*, *Valvata macrostoma*, *Amnicola taylori*, *Pisidium conventus*, etc.) we have a certain number with specialised habitats (*Planorbis glaber*, *Limnaea glabra*, *Physa hypnorum*, *Unio margaritifer*, *Sphaerium pallidum*, *Pisidium lilljeborgii*, *P. personatum*), and besides some 40 species of which it might be said with rather vague monotony that they live in "rivers, canals, streams or ponds" or some such combination—at any rate by anyone whose standard of experience was based on collecting in the southern half of England.

Ancylus fluviatilis	A	B	C	D	*Valvata piscinalis*	A	B	C	D
A. lacustris	A	.	C	D	*V. cristata*	A	.	C	D
Limnaea peregra	A	B	C	D	*Paludestrina jenkinsi*	.	B	.	.
L. auricularia	(A)	B	C	D	*Neritina fluviatilis*	A	B	.	D
L. stagnalis	A	B	C	D	*Anodonta cygnea*	.	B	C	D
L. palustris	A	B	C	D	*A. anatina*	.	B	.	.
Planorbis corneus	.	B	C	D	*Unio pictorum*	.	B	.	D
Pl. complanatus	A	B	C	D	*U. tumidus*	.	B	.	D
Pl. carinatus	A	.	.	.	*Sphaerium corneum*	A	B	C	D
Pl. albus	A	B	C	D	*S. lacustre*	.	B	.	.
Pl. nautileus	A	.	.	.	*S. rivicola*	.	B	.	.
Pl. vortex	A	.	C	D	*Pisidium amnicum*	A	B	C	D
Pl. spirorbis	A	.	.	D	*P. cinereum*	A	B	.	D
Pl. contortus	A	.	C	D	*P. henslowanum*	.	B	C	D
Pl. fontanus	A	.	C	D	*P. hibernicum*	A	.	C	.
Physa fontinalis	A	B	C	.	*P. milium*	A	.	C	D
Paludina contecta	.	.	.	D	*P. nitidum*	A	B	C	D
P. vivipara	.	B	.	.	*P. obtusale*	A	.	.	.
Bithinia tentaculata	A	B	C	D	*P. pulchellum*	A	.	C	D
B. leachii	.	B	C	D	*P. subtruncatum*	A	B	C	D

A, Lough Rea; B, Grand Junction Canal; C, R. Colne backwater; D, R. Nene.

As with the land Mollusca, these sorts with generalised habitats may be arranged in a scale, at one end of which are tolerant species which may not

infrequently be found by themselves or with few companions and tend to have a wide geographical range, while at the other are exacting species which commonly have a number of others living with them which are equally or less particular and have a more restricted distribution. *Limnaea peregra*, *Planorbis albus*, *Pl. contortus*, *Sphaerium lacustre*, *Pisidium cinereum* are tolerant species; *Limnaea auricularia*, *Planorbis corneus*, *Paludina contecta*, *Bithinia leachii*, *Pisidium amnicum* are exacting species; *Limnaea stagnalis*, *Planorbis complanatus*, *Bithinia tentaculata*, *Pisidium subtruncatum* are intermediate. Since the tolerant species have no objection to living in the loci required by the exacting, the goodness or badness of a habitat may be pragmatically measured either by the number of species living there or by their quality: any place with more than 20 kinds or with one or more exacting species may be accepted as being "good".

If the foregoing discussion of the relevant qualities of habitats in any way represents the facts, we should expect to find most sorts and more of the "choosey" species in a good-sized locus, in parts too deep for the growth of plants, but with adequate vegetation at the gently shelving edges, well exposed to sunlight, in the south-east of England and charged with slowly flowing, clear, calcareous water. Such a habitat, and many of its subvarieties, is provided by the R. Thames, and no doubt in the main river and its various branches and diverticula at, for example, Oxford all the 40 species in the list on p. 171 can be found, and in addition *Planorbis acronicus*, *Pseudanodonta*, *Pisidium torquatum*, *P. personatum*, *P. supinum* and *P. tenuilineatum*—in all about 45. Another very rich locus is the calcareous L. Rea in the Galway limestone described by R. A. Phillips (**193**) who has been good enough to give me the detailed list of 30 species: 27 of them are marked A on p. 171, and there are in addition *Planorbis glaber*, *Pisidium lilljeborgii* and *P. personatum*; *Limnaea auricularia* occurs in a small communicating lake and *Physa hypnorum* in drains entering the lake. Considering that *Paludina*, *Unio pictorum*, *U. tumidus* and *Sphaerium rivicola* do not occur in Ireland, this is a remarkable list and only *Paludestrina jenkinsi*, *Anodonta cygnea* and *Pisidium henslowanum* are absent of those which might reasonably be looked for. It should be compared with the list of 17 species for L. Leane (above, p. 151), 85 miles away, which is equally favourable in its position and configuration, but contains soft water instead of hard. Oldham's list for the Grand Junction (now the Grand Union) Canal at Berkhamsted includes 27 sorts marked B on p. 171, and also *Dreissena*, *Pisidium torquatum* and *P. supinum*, while *Pseudanodonta*, *Sphaerium pallidum*, *Pisidium hibernicum*, *P. milium* and *P. tenuilineatum* live in the canal not far off, i.e. about 34 species. As a fourth example of a rich habitat we may take a quiet backwater of the R. Colne with 26 species marked C. Llangorse Lake (p. 156) and Rostherne Mere (p. 164) also contain as many as 25 kinds.

As a habitat fails to have the combination of good qualities which results

in such prolific yields, so its content in snails diminishes. If the water is quite soft, we expect at the best less than 20 species (above, p. 151) and the exacting ones disappear. If the water is stagnant, 10 is a good number; if it is shaded 5 or less, and so on until we come down to the poorest places with nothing but *Pisidium cinereum* or some other tolerant species. Examples of these have been already given.

(*a*) *Rivers*

Rivers such as the Thames which are calcareous, naturally quiet and have in many instances been canalised and tamed, are fruitful enough, and most slow south-eastern rivers will yield pretty well: Kendall (**230**) gives a list of 32 kinds for the R. Nene in Northampton marked D on p. 171, with the addition of *Dreissena* and *Pisidium supinum*. But as a class they are not very good habitats: a calcareous river such as the R. Tees in the neighbourhood of Barnard Castle (calcium 32) may be too swift for anything nobler than *Limnaea peregra* and *Ancylus fluviatilis*, and many soft-water rivers in the north and west contain even less. The chief difficulties seem to be that the current is too fast, the quiet places too deep, and the shallow places too rapid, the banks go straight down without shelving and the whole is liable to be periodically scoured out with floods. These are the defects of the Herefordshire Wye which, with water just on the "hard" limit (calcium 23), contains only some 19 species with a striking deficiency in pulmonates:

Ancylus fluviatilis	*Unio pictorum*	*Pisidium henslowanum*
Limnaea peregra	*U. tumidus*	*P. nitidum*
Bithinia tentaculata	*U. margaritifer*	*P. pulchellum*
Valvata piscinalis	*Sphaerium corneum*	*P. subtruncatum*
Paludestrina jenkinsi	*Pisidium amnicum*	*P. supinum*
Neritina fluviatilis	*P. cinereum*	*P. torquatum*
Anodonta anatina		

Streams and brooks are also poor places unless they flow through ponds or have quiet bays in which plants can grow and Mollusca do something else than hang on in the current. In the absence of plants, *Planorbis* sometimes gets protection under stones as *Bithinia tentaculata* may do.

(*b*) *Canals*

Canals luckily reproduce the qualities of the best rivers, and are of such interest that they deserve fuller notice. Apart from a few ancient waterways such as the Foss Dyke in Lincolnshire, which was made by the Romans, and the Exeter ship canal, which is Elizabethan, the first modern canal was built by Francis Egerton, third duke of Bridgwater (1736–1803), who is commemorated by the monument erected in 1832 to "the father of inland navigation", which looks out from the chalk escarpment at Ashridge over the reservoirs of the Grand Junction Canal which joins the Thames to the central plain of England. Disappointed in a matrimonial enterprise in London, he retired to his estates in Lancashire, and with the aid of Brindley the canal from Worsley to Manchester to carry coal from his pits was opened in 1761.

The Manchester to Liverpool canal followed and gave such a demonstration of the commercial possibilities of this new form of transport that canals were projected and executed with great enthusiasm all over the country, ultimately, with the canalised rivers, reaching a length of about 3800 miles (about 18 times the length of the Thames). Most of them were made before 1800 after which progress became slower and finally the boom died out as good roads and railways developed: practically nothing fresh has been done since about 1830. Much information and some excellent maps will be found in the reports of the Canal Commission of 1909. The "lodes", "levels" and draining ditches of the fens in Cambridge, Norfolk and Lincoln and the Somerset "rhines" were made for another purpose and date from various periods, chiefly the seventeenth century: conchologically they are equivalent to canals detached from the main system.

The Canal Basin

Fig. 63.

Canals are important to us because they have joined up all the river basins of central England and have provided a particularly favourable type of habitat. They communicate in one way or another with most of the rivers with which they come in contact, and about the middle of last century a snail could start in the Thames at London and travel in uninterrupted water to Norfolk or Leeds or Kendal or Newtown in Montgomery or Hereford or Trowbridge, or by slipping into the upper waters of the Avon in the vale of Pusey even to Christchurch or Southampton: the area open to it, which may conveniently be called the "canal basin", is roughly shown in Fig. 63, where it is if anything too small. These facilities have since to some extent deteriorated: the Gloucester and Hereford canal was drained and abandoned just when I began to collect shells, and I have a vivid recollection of its wealth, for it was by far the richest locus in the county; the Tenbury and Leominster canal was then only a grassy groove; the Wilts and Berks canal has long been derelict and a more important link, the Thames and Severn canal, has now been abandoned in its upper parts though the two rivers are still in communication via Oxford and the midlands. But the main system still survives in continuity and will presumably continue even if out of use so long as it needs no trouble to keep it full of water. In Scotland canals have done little to upset the natural arrangements, but in Ireland the Grand and Royal canals have united the main river basins and joined Belfast and L. Neagh with the R. Erne, the R. Shannon, Dublin and the R. Barrow in the south.

As habitats canals are better than they often look. If they are in active

use the water is probably turbid, water weeds are abundant only in quiet recesses, there may be oil and scum on the surface and the bottom may be stony or even largely composed of cinders. But they are always worth examination, and it is surprising how abundant Mollusca may be in places which have a thoroughly dirty and unprepossessing appearance. This is due to their having a good volume of water with a steady slow and never violent flow; the water-level remains almost constant and there are no floods. The rate of flow varies with the differences of level, the number of locks and the frequency with which they are used: the Grand Junction Canal falls 420 ft. in 40 miles from Tring to Brentford and about half as much in the opposite direction, whereas the R. Thames falls 315 ft. in 158 miles from Ewen to London and the R. Severn 180 ft. in 90 miles from Shrewsbury to Gloucester. Locks, leaking or working, do a good deal to aerate the water: those at Tring, which are fairly busy, use about 3 million gallons a day or about 1/400 of the flow of the Thames and 1/6 of that of the R. Lark. Jackson (**186**) points out that the Polyzoa, *Plumatella* and *Fredericella*, and the sponge, *Ephydatia fluviatilis*, which are sensitive indicators of adequate oxygenation, are abundant in the foul-looking Manchester canals. The rush of water and the recesses by locks also provide good patches of mud and silt for bivalves. The southern and midland canals all contain hard water: it may be soft in some places in the north. Hot engine water is sometimes discharged into them which the Mollusca seem to like, but we have no species for which it is necessary.

Hence canals as a class are the richest habitats we have. Lists of more than 30 species from the Grand Junction and Shropshire Union canals have been already given (above, pp. 171, 160), and conditions evidently favour bivalves, operculates and pulmonates alike. The difference is, however, chiefly seen in the larger bivalves and operculates for which many districts provide few suitable natural habitats. Thus Davies (**187**) in a thorough survey of the smoke-begrimed built-up district round Eccles to the west of Manchester found 27 species in the two canals, 22 of them in the historic Bridgewater canal:

Limnaea peregra	*Physa fontinalis*	*Sphaerium corneum*
**L. auricularia*	**Ph. acuta*	*Sph. lacustre*
L. stagnalis	**Bithinia tentaculata*	**Sph. pallidum*
L. palustris	**Valvata piscinalis*	**Pisidium amnicum*
Planorbis carinatus	*Paludestrina jenkinsi*	*P. cinereum*
Pl. albus	**Anodonta cygnea*	*P. henslowanum*
**Pl. dilatatus*	**Unio tumidus*	*P. milium*
Pl. vortex	**Dreissena polymorpha*	*P. nitidum*
Pl. fontanus	**Sphaerium rivicola*	*P. subtruncatum*

The 11 species marked * occurred only in the canals and in none of the numerous ("upwards of a hundred") ponds and ditches in the neighbourhood which in their turn showed 9 species (*Limnaea glabra*, *Planorbis corneus*, *Pl. complanatus*, *Pl. nautileus*, *Pl. spirorbis*, *Pl. contortus*, *Physa hypnorum*, *Pisidium obtusale* and *P. personatum*) which were not found in the canals.[1]

[1] These data also illustrate the relative immunity of water snails to smoke: the same district had only 20 sorts of land Mollusca with nothing more fastidious than *Helix hispida*.

Similarly, Alkins (**50**) says that 8 of the 30 species found in his district in north Staffs. occur only in the canal (*Ancylus lacustris*, *Limnaea auricularia*, *Planorbis corneus*, *Physa fontinalis*, *Paludina vivipara*, *Valvata piscinalis*, *Sphaerium rivicola* and *Pisidium amnicum*). Ellis (**280**) lists 25 species *plus Pisidium* from Leicestershire, and Hargreaves and Firth (**189**) give another typical collection from the Wakefield canal:

Limnaea peregra	*Physa fontinalis*	*Pseudanodonta* sp.
L. stagnalis	*Bithinia tentaculata*	*Unio pictorum*
L. palustris	*Valvata piscinalis*	*U. tumidus*
Planorbis corneus	*Neritina fluviatilis*	*Sphaerium corneum*
Pl. complanatus	*Anodonta cygnea*	*Sph. rivicola*
Pl. vortex	*A. anatina*	*Pisidium amnicum*

Taking the whole British list there are, I think, only 6 species which have not been recorded for canals (*Limnaea glabra*, *Pisidium conventus*, *Planorbis glaber*, *Pl. vorticulus*, *Segmentina nitida* and *Valvata macrostoma*), and it is about equally true that these have not been found in rivers either while the last 4 occur in, and the last 3 are characteristic of, large draining ditches which are equivalent in nature and origin to canals. Even *Unio margaritifer* is recorded by Jeffreys (**141**, p. 38) from the Swansea canal, and *Pisidium lilljeborgii* by Oldham and Stelfox in the Shropshire Union canal near Llangollen.

That one of the essential virtues of canals is the flow of water is shown by the poor fauna of the stagnant remains of abandoned undertakings which may be so choked with vegetation and the products of its decomposition that they are less productive than good ponds: Bowell (**211**) noted the same in the Grand Western Canal in Devon.

How far the continuity of this canal-river system has enabled Mollusca to spread through England is impossible to say, for the canals anticipated any accurate knowledge of distribution: da Costa (**190**) in 1778 naturally makes no mention of them, and his field work is poor and many of his localities dubious; Montagu (**35**) in 1803 mentions "the canal intended to make a junction of the Kennet and Avon" only as the place where he found "*Helix fragilis*", though his path from Lackham House to the wood where he first found *Ena montana* crossed the route of the Wilts and Berks canal as well as the R. Avon in which he found many species: both canals were put in hand about 1795, and in 1799 Montagu had gone to Kingsbridge. Turton (**191**) in 1831 mentions them several times, but in no significant connection. But it seems very likely that they have helped *Sphaerium pallidum* and *Dreissena* to spread from the metropolitan area, as the operculate *Lithoglyphus naticoides* has passed from the Danube via Ludwig's canal to Holland and France (**77**, p. 656). The distribution of a number of species (Figs. 40–42, 44–48) which are fond of canals is also curiously similar to the canal basin (Fig. 63):

Bithinia leachii	*Unio pictorum*	*Sphaerium rivicola*
Paludina vivipara	*U. tumidus*	*Sph. pallidum*
P. contecta	*Dreissena polymorpha*	

In Ireland *Bithinia leachii* is almost restricted to the Grand and Royal Canals and the communicating R. Barrow (**62**, **192**, **193**).

It is, too, evident that on a smaller scale continuity and suitability have extended several species beyond their natural range, and it seems certain that it is along the Shropshire Union Canal that *Limnaea auricularia*, *Planorbis corneus* and *Bithinia leachii* have reached Denbigh and *Planorbis corneus*, *Paludina vivipara*, *Unio pictorum*, *U. tumidus*, *Dreissena* and *Sphaerium pallidum* have spread to Montgomery, which in its natural state contains no appropriate habitats. Similarly the old canal was responsible for *Limnaea auricularia*, *Paludina vivipara*, *Dreissena* and possibly *Limnaea stagnalis* in Herefordshire.

Detached canals which communicate only with local rivers and the sea give various results, but they also illustrate the importance of a good habitat. The Tiverton Canal is overgrown and stagnant and it contains nothing of note except *Limnaea auricularia* (F. F. Laidlaw). The remnants of the Bude canal yielded *Anodonta anatina* and *Pisidium torquatum* as well as ordinary species. The Newport and Brecon Canal has *Paludina vivipara*, which might, I suppose, have somehow survived a sea passage on a barge from Gloucester, and so have the Cardiff and Exeter (**144**) Canals, so that the five most westerly occurrences of that species are in canals with which Tate (**247**, p. 55) thinks it is particularly associated. The Exeter Canal and the canalised R. Exe have also *Limnaea auricularia*, *Planorbis corneus*, *Dreissena* and *Sphaerium rivicola*, and how these characteristic canal species got so far west of their nearest habitats is unknown; the canal is accessible only to ocean-going shipping, and the projected conjunction of the Exe with the Somerset rivers *via* the Grand Western Canal was never completed: somehow or other the appropriate Mollusca seem in the end to reach suitable habitats, and in this instance they have had 350 years to do it in. The eastern end of the Forth and Clyde Canal has provided the only Scotch loci for *Bithinia leachii* and *Amnicola taylori* (**101**). *Limnaea stagnalis* was first found in Glamorgan in the Cardiff Canal in 1915 since when it has spread freely in the neighbourhood (J. D. Dean).

(*c*) *Lakes*

Most natural *lakes* are relatively unproductive because they belong to the type which has come to be called "mountain" (or "highland"): their essential quality is not, however, that they lie at high altitudes, for they are found in barren soils at sea-level, but that, as Tansley (**195**) points out in discussing the vegetation, they contain soft water. Altitude increases their austerity because, apart from climate, the lakes nearer the summits have the softer water which is indeed in some instances not far from distilled water. In extreme cases there is no phanerogamic vegetation and no macroscopic life: with rather more dissolved salts a sparse vegetation appears with characteristic plants such as *Lobelia dortmanna*, *Isoetes* and *Subularia*, and as conditions improve we find perhaps *Littorella*, *Potamogeton natans*, *Myriophyllum* and the small water-lilies. But the total quantity of plants remains very small and the floor is mostly made up of rocks and stones with a few patches of silt and humus

in which *Pisidium* live. In such places, with a calcium content of about 5 mg. per litre or less, *Pisidium cinereum*, *P. hibernicum*, *P. lilljeborgii* and *P. nitidum* are fairly common, *P. milium*, *P. obtusale* and *P. subtruncatum* rather less frequent, *Limnaea peregra* and *Ancylus fluviatilis* are not rare on the stones and *Planorbis albus*, *Pl. contortus* and *Sphaerium corneum* occur occasionally. With equal amounts of lime, the fauna is likely to be richer at low altitudes than up in the mountains. As Pearsall (**136**) shows, a complete gradation can be traced from the primitive barren lakes to such places as Windermere or L. Leane (above, p. 151), where with calcium about 10 or rather less there is much more vegetation and humus and a good many Mollusca (*Valvata piscinalis*, *Physa fontinalis*, etc.).

If the water is calcareous, the lake may, as at Malham Tarn, continue to have a bare "highland" appearance with a richer snail fauna, or the whole character of the place may change, as at Bwch Llyn which, while climatically perhaps "highland", is floristically and conchologically a "lowland" lake, and through such habitats as Llangorse Lake (above, p. 156) grades into the lakes and reservoirs which occur in lowland cultivated country, have calcareous water and are mostly good places for Mollusca, though they do not figure much in the literature or our experience because of their scarcity, and because they are so often spoiled by being denatured in various ways such as stocking with ornamental birds or killing the "weeds" with copper sulphate (which is excessively poisonous (**201**) to snails) or by mechanical disturbance (e.g. by boating) which water snails dislike as much as land Mollusca. What such habitats can produce under favourable conditions is shown by L. Rea (above, p. 171), and as an example of a mediocre fauna I give the list for the Elstree Reservoir (59 acres) in Herts which was made about 130 years ago:

Limnaea peregra	*Planorbis nautileus*	*Sphaerium lacustre*
L. auricularia	*Pl. vortex*	*Pisidium cinereum*
L. stagnalis	*Pl. spirorbis*	*P. nitidum*
Planorbis corneus	*Anodonta cygnea*	*P. obtusale*
Pl. complanatus	*Unio pictorum*	*P. subtruncatum*
Pl. albus	*Sphaerium corneum*	

The nomenclature is obviously unsatisfactory because it attempts to describe oecological categories in lay terms: "mountain" and "lowland" might well be replaced by "non-calcareous" (calcium under 10) and "calcareous" (calcium over 20), and the nature of the water can probably in most cases be deduced from the snails and plants (**284**) present.

6. Summary and conclusions

Water Mollusca are not dependent on other animals except that *Anodonta* and *Unio* have an obligatory parasitic phase on fish. Nor have they any specific foods. There are indications that the habitats of a few species are partly determined by competition with other Mollusca, but in general this is unimportant and most of the species which occur in the worst places are

found also in the best. Hence each species can live in any place where its characteristic needs are met by the physical and chemical conditions. The more important features of favourable habitats are (1) cleanliness of water, (2) absence of disturbance, and (3) presence of lime: other factors such as rate of flow, volume of locus, vegetation, etc., are of moment because of their influence on the first two. Bivalves, operculates and pulmonates can each be divided into a group which can live in soft as well as hard water and one which ordinarily needs a fair amount of lime: also into those which can tolerate stagnant water (which include no operculates) and those which need clean and usually running water. With a few exceptions, the needs of the species are so similar that habitats can be classed as good or bad for Mollusca as a whole: the richest places are calcareous rivers, lakes and canals, the poorest rapid streams, mean ponds and mountain lakes.

This paper has, I hope, asked more questions than it has answered. The descriptive phase of the study of the habitats of Mollusca is far from complete but it has reached the point where it suggests explanations and general principles which are open to analysis, and, though there is still room for collecting at large, field work is likely to be more fruitful if it is planned to throw light on definite problems and guided by some theory. It may centre round the study of particular habitats or of particular species, and since the Mollusca have so little direct relation to one another or to other animals it will mostly be concerned with the investigation of the environment, and ideas which arise in the field may in many instances be tested by experiments in aquaria and by well-considered transplantations.

My information about geographical distribution and localities is largely derived from the accumulation of data made with such devotion by W. D. Roebuck for J. W. Taylor's *Monograph* and for his own *Census of Distribution*, maintained since his death by the Conchological Society. The maps are based on the *Census* records with the addition of a few reported occurrences which seemed sufficiently credible, although no actual specimens have been verified by the Society's referees.

REFERENCES

1. **Latter, O. H. (1904).** "Natural history of some common animals.'
2. **Warrington, R. (1852).** Ann. Mag. Nat. Hist. 10: 274.
3. **Welch, R. (1934).** J. Conch. 20: 81.
4. **Sherborn, C. D. (1882).** Science Gossip, p. 262.
5. **Cockerell, T. D. A. (1883).** Nat. Hist. Notes, 3: 48.
6. **Turner, F. M. (1926).** Naturalist, p. 231; **(1927)** Essex Nat. 22: 48.
7. **Boycott, A. E. (1919),** Trans. Herts. Nat. Hist. Soc. 17: 153; **(1918)** J. Conch. 15: 240.
8. **Boycott, A. E. (1921).** Trans. Herts. Nat. Hist. Soc. 17: 263.
9. **Boycott, A. E. (1930).** Trans. Herts. Nat. Hist. Soc. 19: 1.
10. **Bloomer, H. H. (1930).** Proc. Malac. Soc. 19: 10; **(1934)** 21: 21; **(1935)** 21: 304.
11. **Boycott, A. E., Diver, C., Garstang, S. L.** and **Turner, F. M. (1930).** Phil. Trans. Roy. Soc. B, 219: 51.
12. **Oldham, C. (1930).** Naturalist, p. 177; **(1929)** J. Conch. 18: 298.
13. **Larambergue, M. (1929).** C. R. Acad. Sci., Paris, 189: 1027.

14. **Ritchie, J.** (**1920**). "The influence of man on animal life in Scotland."
15. **Oldham, C.** (**1931**). J. Conch. 19: 179.
16. **Cooke, A. H.** (**1895**). Molluscs (Camb. Nat. Hist.).
17. **Baker, F. C.** (**1911**). "Limnaeidae of North and Middle America."
18. **Baker, F. C.** (**1928**). "Freshwater Mollusca of Wisconsin."
19. **Gurney, R.** (**1933**). "British freshwater Copepoda," 3: 316, 338.
20. **Dodgson, R. W.** (**1928**). "Report on mussel purification." H.M. Stationery Office, London.
21. **Allen, C.** (**1935**). J. Conch. 20: 126.
22. **Cleave, H. J.** and **Lederer, L. G.** (**1932**). J. Morph. 53: 499; (**1934**) Ecology, 15: 17.
23. **Krull, W. H.** (**1933**). J. Wash. Acad. Sci. 23.
24. **Oldham, C.** (**1885**). Naturalist, p. 274; **Lawson, A. K.** (**1920**) Lancs Nat. 12: 272; (**1921**) J. Conch. 16: 144.
25. **Carter, C. S.** (**1918**). Naturalist, p. 24.
26. **Bellamy, J. C.** (**1839**). "The natural history of South Devon."
27. **Hall, C. B.** (**1933**). "The culture of fish in ponds." H.M. Stationery Office, London.
28. **Boycott, A. E.** and **Bowell, E. W.** (**1898**). Trans. Woolhope Nat. Field Club, p. 91.
29. **Jeffery, W.** (**1882**). J. Conch. 3: 309; **Welch, R. J.** (**1904**) Irish Nat. 13: 45.
30. **Fysher, G.** (**1925**). Naturalist, p. 342.
31. **Harding, W. H.** (**1910**). Parasitology, 3: 130.
32. **Baldwin, E.** (**1935**). J. Exp. Biol. 12: 29; **Rajat, H.** (**1917**) C. R. Acad. Sci., Paris, 80: 172.
33. **Pentelow, F. T. K.** (**1932**). J. Anim. Ecol. 1: 101.
34. **Slack, H. D.** (**1934**). J. Anim. Ecol. 3: 105.
35. **Montagu, G.** (**1803**). "Testacea britannica."
36. **Reid, C.** (**1892**). Trans. Norfolk and Norwich Nat. Soc. 5: 272; (**1911**) Naturalist, p. 377.
37. **Oldham, C.** (**1926**). J. Conch. 18: 17; (**1927**) *ibid.* 18: 70; **Walton, C. L.** (**1913**) N.W. Nat. 8: 326.
38. **Oldham, C.** (**1928**). J. Conch. 18: 272.
39. **Fritch, F. E.** and **Salisbury, E. J.** (**1920**). "Introduction to the structure and reproduction of plants."
40. **Boycott, A. E.** (**1927**). Proc. Malac. Soc. 17: 156.
41. **Laver, H.** (**1882**). Trans. Epping Forest Nat. Field Club, 2: 88.
42. **Elton, C.** (**1933**). "The ecology of animals."
43. **Müller, O. F.** (**1774**). "Vermium historia."
44. **Nelson, W.** (**1891**). Naturalist, p. 273; (**1899**) *ibid.* pp. 45, 77, 363; (**1880**) J. Conch. 3: 115; (**1888**) *ibid.* 5: 262.
45. **Coates, H.** (**1922**). Trans. Perth Soc. Nat. Sci. 7: 47.
46. **Alkins, W. E.** (**1918**). J. Conch. 15: 284; (**1919**) *ibid.* 16: 23.
47. **Roebuck, W. D.** (**1918**). Scot. Nat. p. 113.
48. **Wood, A.** (**1897**). "Mollusca of Sutton Coldfield."
49. **Stelfox, A. W.** (**1918**). J. Conch. 15: 292; (**1929**) Proc. Roy. Irish Acad. 39 B: 8.
50. **Alkins, W. E.** (**1920–21, 1922–23, 1924–25**). Trans. N. Staffs Field Club (reprints).
51. **Favre, J.** (**1927**). Mém. Soc. Phys. et Hist. Nat. Genève, 40: 171; (**1935**) *ibid.* 41: 295.
52. **Jenyns, L.** (**1846**). "Observations in natural history," p. 319.
53. **Butcher, R. W.**, **Pentelow, F. T. K.** and **Woodley, J. W. A.** (**1930**). Ministry of Agriculture: Fishery investigations, 3: no. 3.
54. **Stelfox, A. W.** (**1909**). Irish Nat. 18: 91.
55. **Ellis, A. E.** (**1925**). J. Conch. 17: 219.
56. **Davies, W. H.** (**1918**). Lancs Cheshire Nat. 11: 73.
57. **Jackson, J. W.** (**1920**). Lancs Cheshire Nat. 13: 92.
58. **Collinge, W. E.** (**1891**). Naturalist, p. 78.
59. **Adams, L. E.** (**1896**). "Collector's Manual Brit. L.F.W. Shells," ed. 2, p. 133.
60. **Ashford, C.** (**1887**). J. Conch. 5: 157.
61. **Kew, H. W.** (**1886**). Naturalist, p. 79.
62. **Stelfox, A. W.** (**1910**). Irish Nat. 19: 240.

63. **Oldham, C. (1930).** Ibis, p. 239.
64. **Adams, L. E. (1893).** Naturalist, p. 316.
65. **Shrubsole, G. W. (1886).** J. Conch. 5: 70.
66. **Frierson, L. S. (1923).** Nautilus, 36: 43.
67. **Geyer, D. (1927).** "Unsere Land- und Süsswasser Mollusken," ed. 3, p. 187.
68. **McKean, K. (1882–3).** Proc. Croydon Micro. Nat. Hist. Club, p. 145.
69. **Haas, F. (1910).** Proc. Malac. Soc. 9: 109.
70. **Phillips, R. A. (1928).** Proc. Malac. Soc. 18: 69.
71. **Jackson, J. W. (1925).** J. Conch. 17: 195.
72. **Regan, C. T. (1911).** "The fresh-water fishes of the British Isles," p. 189.
73. **Kew, H. W. (1893).** "The dispersal of shells."
74. **Kennard, A. S. (1923).** Proc. Malac. Soc. 15: 251.
75. **Gray, J. E. (1856).** Ann. Mag. Nat. Hist. 17: 465.
76. **Kennard, A. S.** and **Woodward, B. B. (1917).** Proc. Geol. Ass. 28: 19.
77. **Germain, L. (1931).** "Mollusques terrestres et fluviatiles de France."
78. **Oldham, C. (1932).** J. Conch. 19: 271.
79. **Evans, W. E. (1918).** Scot. Nat. p. 71.
80. **Stelfox, A. W. (1915).** Irish Nat. 24: 34; **Tomlin, J. R. (1910)** J. Conch. 13: 79.
81. **Hey, W. C. (1887).** Nat. World, 4: 22.
82. **Stelfox, A. W. (1929).** Proc. Roy. Irish Acad. 39: 8.
83. **Phillips, R. A.** and **Stelfox, A. W. (1918).** Irish Nat. 27: 33.
84. **Milne, J. G.** and **Oldham, C. (1894).** J. Conch. 7: 323; **Hargreaves, J. A. (1909)** *ibid.* 12: 307; **Glover, T. (1887)** *ibid.* 5: 232; **Jackson, J. W. (1918)** Lancs Cheshire Nat. 11: 71; **(1920)** *ibid.* 13: 33; **Standen, R. (1887)** Naturalist, p. 160; **Oldham, C. (1896)** *ibid.* p. 124.
85. **Britten, H.** and **Williams, E. G. (1934).** Northw. Nat. 9: 21; **Standen, R. (1887)** Naturalist, p. 160.
86. **Welch, R. (1908).** Irish Nat. 17: 1.
87. **Oldham, C. (1921).** J. Conch. 16: 155; **(1922)** *ibid.* 16: 251; **(1926)** *ibid.* 18: 36; **Ellis, A. E. (1931)** *ibid.* 19: 177 and 258.
88. **Taylor, F. (1898).** J. Conch. 9: 52.
89. **Adams, L. E. (1890).** J. Conch. 6: 278.
90. **Smith, E. A. (1889).** J. Conch. 6: 142.
91. **Daniel, A. T. (1894).** J. Conch. 7: 325.
92. **Hann, A. (1898).** J. Conch. 9: 89.
93. **Taylor, F. (1900).** J. Conch. 9: 340.
94. **Kennard, A. S.** and **Woodward, B. B. (1899).** Proc. Malac. Soc. 3: 298.
95. **Boycott, A. E. (1919).** J. Conch. 16: 54; **Robson, G. C. (1923)** Brit. J. Exp. Biol. 1: 65; **Quick, A. E. (1920)** J. Conch. 16: 97.
96. **Needham, J. (1935).** Biochem. J. 29: 238.
97. **Ellis, A. E. (1925).** Ann. Mag. Nat. Hist. 15: 496.
98. **Humphreys, G. (1911).** J. Conch. 13: 254.
99. **Welch, R. J. (1931).** Irish Nat. J. 3: 198; **Robinson, J. F. (1926)** Naturalist, p. 87; **Kew, H. W. (1902)** *ibid.* p. 270; **MacDonald, R. (1932)** J. Conch. 19: 262 (at 500 ft.); **Crapper, E. (1924)** *ibid.* 17: 137.
100. **Stubbs, A. G. (1903).** J. Conch. 10: 284 and in **Taylor** MS.
101. **Waterston, A. R. (1934).** J. Conch. 20: 55.
102. **Jackson, J. W.** and **Taylor, F. (1904).** J. Conch. 11: 9; **Taylor, F. (1918)** Lancs Cheshire Nat. 11: 19.
103. **Stelfox, A. W. (1911).** Proc. Roy. Irish Acad. 29 B: 65.
104. **Moquin-Tandon, A. (1855).** "Hist. Nat. Moll. terrest. fluviat. France."
105. **Moore, C. H. (1906).** J. Conch. 11: 266.
106. **Heathcote, W. H. (1924).** J. Conch. 17: 185.
107. **Oldham, C. (1933).** J. Conch. 19: 330.
108. **Pigeon, D. (1874).** J. Conch. 1: 55; **Cooper, J. E. (1912)** *ibid.* 13: 273; **Marquand, E. D. (1912)** *ibid.* 13: 340; **Ashford, C. (1887)** *ibid.* 5: 157; **Wotton, F. W. (1886)** *ibid.* 5: 53;

Wood, A. (ref. 48 above); **Jeffreys, J. G.** (**1862**) Brit. Conch. 1: 120; **Unwin, W. C.** (**1853**) Naturalist, 3: 54; **Ashford, C.** (**1887**) Nat. Hist. J. 11: 125; **Whitehead, H.** (**1935**) J. Anim. Ecol. 4: 70.

109. **Wilson, C. B.** (**1916**). Bureau of Fisheries Document, 824, p. 347.
110. **Harms, F.** (**1907**). Zool. Anz. 31: 814.
111. **Boycott, A. E.**, **Oldham, C.** and **Waterston, A. R.** (**1932**). Proc. Malac. Soc. 20: 105.
112. **Ashford, C.** (**1879**). J. Conch. 2: 6.
113. **Ashford, C.** (**1900**). Irish Nat. 9: 48; **Green, W. A.** (**1901**) *ibid.* 10: 132.
114. **Blackburn, E. P.** (**1931**). J. Conch. 19: 130; **Lucas, B. R.** (**1903**) *ibid.* 10: 279.
115. **Fierke, F. W.** (**1890**). J. Conch. 6: 251; **Cooper, J. E.** (**1931**) *ibid.* 19: 113 and 180; **Kew, H. W.** (**1903**) Naturalist, p. 263.
116. **Welch, R.** (**1901**). Irish Nat. 10: 131; (**1930**) Irish Nat. J. 3: 134; (**1933**) *ibid.* 4: 200; **Fisher, N.** (**1930**) *ibid.* 3: 90; **Oldham, C.** (**1896**) Naturalist, p. 122; (**1908**) *ibid.* p. 259; **Standen, R.** (**1887**) *ibid.* p. 164; **Hudson, B.** (**1886**) J. Conch. 5: 46.
117. **Unwin, W. C.** (**1853**). Naturalist, p. 57.
118. **Taylor, F.** (**1917**). Lancs Cheshire Nat. 10: 214; **Jackson, J. W.** (**1918**) *ibid.* 11: 70.
119. **Jackson, J. W.** and **Kitchen, J. G.** (**1919**). Lancs Cheshire Nat. 12: 131.
120. **Morgan, J. B.** (**1887**). J. Conch. 5: 217.
121. **Cooper, J. E.** and **Loydell, A.** (**1909**). Proc. Malac. Soc. 8: 228.
122. **Taylor, J. W.** (**1879**). J. Conch. 2: 244; **Hey, W. C.** (**1879**) *ibid.* 2: 311; **Roebuck, W. D.** (**1883**) *ibid.* 4: 13; (**1906**) Naturalist, p. 423; (**1918**) *ibid.* p. 262; (**1921**) *ibid.* p. 377; **Saunders, T. W.** (**1926**) *ibid.* p. 220.
123. **Wilcox, H. A.** (**1933**). "The woodlands and marshlands of England."
124. **Macgillivray, W.** (**1843**). "The molluscous animals of Aberdeen, Kincardine and Banff," p. 112.
125. **Salisbury, A. E.** (**1916**). J. Conch. 15: 96.
126. **Rae, W. D.** (**1891**). Science Gossip, 27: 89.
127. **Ridley, H. N.** (**1930**). "The dispersal of plants throughout the world," esp. chap. vi.
128. **Beeston, H.** (**1908**). J. Conch. 12: 191.
129. **White, F. B.** (**1873**). Scot. Nat. 2: 163 and 205.
130. **White, F. B.** (**1881–86**). Proc. Perth Soc. Nat. Sci. p. 114.
131. **Barrow, G.** *et al.* (**1913**). Mem. Geol. Survey Scotland, sheet 64; **Boycott, A. E.** (**1934**) Scot. Nat. p. 7.
132. **Boycott, A. E.** (**1934**). J. Ecol. 22: 1.
133. **Boycott, A. E.** (**1933**). Vasculum, 19: 47.
134. **Martin, E. A.** (N.D.) "Dew ponds," pp. 168, 173.
135. **River Pollution Commission** (**1874**). Sixth report, C. 1112.
136. **Pearsall, W. H.** (**1921**). Proc. Roy. Soc. B, 92: 259.
137. **Moon, H. P.** (**1934**). J. Anim. Ecol. 3: 8; **Burton, F. M.** (**1902**) Naturalist, p. 176; **Kendall, C. E. Y.**, **Dean, J. D.** and **Rankin, W. M.** (**1909**) *ibid.* p. 358; **Roberts, A. W. R.** (**1904**) J. Conch. 11: 24; (**1913**) 14: 82.
138. **Farrer, W. J.** (**1896**). J. Conch. 8: 160.
139. **Standen, R.** (**1898**). Irish Nat. 7: 226.
140. **Oldham, C.** (**1926**). J. Conch. 18: 36.
141. **Jeffreys, J. G.** (**1862**). British Conchology, 1: 102.
142. **Darbishire, R. D.** *et al.* in **Roebuck** MS.
143. **Wotton, F. W.** (**1884**), **Vaughan, J. W.** (about **1902**) and **Oldham, C.** (**1928**) in **Roebuck** MS.; **Vaughan, J. W.** (**1904**) J. Conch. 11: 56; (**1910**) *ibid.* 13: 11; **Phillips, T. R.** (**1926**) "The Breconshire Border."
144. **Parfitt, E.** (**1854**). Naturalist, p. 150; **Marquand, E. D.** (**1889**) J. Conch. 6: 136.
145. **Evans, W.** (**1918**). Scot. Nat. p. 71.
146. **Woodward, B. B.** (**1911**). Proc. Malac. Soc. 9: 5; (**1913**) "Cat. British Pisidium," p. 115.
147. **Annandale, N.** and **Sewell, R. B. S.** (**1921**). Rec. Indian Mus. 22: 243.
148. **Thresh, J. C.** and **Beale, J. F.** (**1925**). "The examination of water and water supplies," ed. 3, p. 338.
149. **Burrell, B. A.** (**1900**). Proc. Yorks Geol. Polyt. Soc. 14: 45.

150. **Soppitt, H. T.** and **Carter, J. W.** (**1888**). Naturalist, p. 91; **Booth, F.** (**1910**) *ibid.* p. 336; **Fysher, G.** (**1929**) *ibid.* p. 207; **Roebuck, W. D.** (**1890**) *ibid.* p. 263; (**1891**) *ibid.* p. 176; (**1884**) J. Conch. 4: 149; **Dean, J. D.** (**1902**) *ibid.* 10: 246.
151. **Boycott, A. E.** (**1934**). Scot. Nat. p. 1.
152. **Stelfox, A. W.** (**1914**). Irish Nat. 23: 126.
153. **Carpenter, K. E.** (**1923**). Nature, 112, 9; cf. ref. 233.
154. **Butcher, R. W., Pentelow, F. T. K.** and **Woodley, J. W. A.** (**1927**). Biochem. J. 21: 945 and 1423; (**1928**) *ibid.* 22: 1035 and 1478.
155. **Kendall, C. E. Y., Dean, J. D.** and **Rankin, W. M.** (**1909**). Naturalist, p. 314; **Roebuck, W. D.** (**1896**) *ibid.* p. 90; **Oldham, C.** (**1903**) J. Conch. 10: 306.
156. **French, J.** (**1899**). Essex Nat. 11: 86.
157. **Gain, W. A.** (**1885**). Science Gossip, 21: 118.
158. **Pearsall, W. H.** and **Hewitt, T.** (**1933**). J. Exp. Biol. 10: 306.
159. **Huggins, H. C.** (**1918**). Irish Nat. 27: 119.
160. **Blackburn, E. P.** (**1934**). Trans. North. Nat. Union, 1: 147.
161. **Carpenter, K. E.** (**1924**). Ann. Appl. Biol. 11: 1; (**1925**) *ibid.* 12: 1; (**1926**) *ibid.* 13: 395; (**1927**) Brit. J. Exp. Path. 4: 378; **Collier, E.** (**1888**) J. Conch. 5: 354.
162. **Beauchamp, R. S. A.** and **Ullyott, P.** (**1932**). J. Ecol. 20: 200; (**1933**) J. Exp. Biol. 10: 113.
163. **Carpenter, K. E.** (**1928**). "Life in inland waters"; (**1927**) J. Ecol. 15: 33.
164. **Gyngell, W.** (**1911**). J. Conch. 13: 178.
165. **Hora, S. L.** (**1934**). Nature, 134, 454; **Anon.** (**1931**) Irish Nat. J. 3: 244.
166. **Arber, A.** (**1920**). "Water plants," p. 298.
167. **Needham, J.** (**1930**). Biol. Zent. 50: 504; (**1931**) "Chemical Embryology," p. 317.
168. **Crowther, H.** (**1896**). J. Conch. 8: 230.
169. **Atkins, W. R. G.** and **Harris, G. T.** (**1924**). Sci. Proc. Roy. Dub. Soc. 18: 1.
170. **Guppy, H. B.** (**1894**). Proc. Roy. Phys. Soc. Edin. 12: 286; (**1897**) 13: 33 and 204; (**1894**) Science Gossip, 1: 145, 178 and 195.
171. **Backrach, E.** and **Cardot, H.** (**1924**). C. R. Soc. Biol. 91: 260 and 1017.
172. **Gain, W. A.** (**1891**). Science Gossip, 27: 118.
173. **Standen, R.** (**1885**). Science Gossip, 21: 238; **Cockerell, T. D. A.** (**1885**) *ibid.* 21: 211.
174. **Peacock, E. A. W.** (**1902**). Naturalist, p. 139.
175. **Standen, R.** (**1887**). Naturalist, p. 159; **Oldham, C.** (**1896**) *ibid.* pp. 110, 125; (**1908**) *ibid.* p. 261.
176. **Dalgliesh, J. G.** (**1933**). J. Conch. 19: 358.
177. **Shrubsole, G. W.** (**1933**). J. Conch. 19: 363; (**1935**) *ibid.* 20: 130.
178. **Bloomer, H. H.** (**1930**). J. Conch. 19: 13.
179. **Welch, R. J.** (**1931**). J. Conch. 19: 119.
180. **Cooper, J. E.** (**1929**). J. Conch. 18: 317.
181. **Lovell, M. S.** (**1867**). "Edible Mollusks," p. 63.
182. **Thiel, M. E.** (**1926**). Mitt. Zool. Staatsinst. Zool. Mus. Hamburg, 42: 40, 48 and 152; **Monk, C. R.** (**1928**) J. Morph. 45: 473.
183. **Oldham, C.** (**1928**). Proc. Malac. Soc. 18: 42; **Boyd, A. W.** (**1934**) Manchester Guardian Dec. 7th.
184. **Fysher, G.** (**1929**). Naturalist, p. 208.
185. **Kendall, C. E. Y.** (**1921**). J. Conch. 16: 244.
186. **Jackson, J. W.** (**1918**). Lancs Nat. 11: 69.
187. **Davies, W. H.** (**1922**). Lancs Cheshire Nat. 14: 263.
188. **Bateman, G. C.** (**1902**). "Freshwater aquaria," ed. 2, p. 253.
189. **Hargreaves, J. A.** and **Firth, J. D.** (**1916**). Naturalist, p. 229.
190. **da Costa, E. M.** (**1778**). "British Conchology."
191. **Turton, W.** (**1831**). "Manual L.F.W. Shells."
192. **Allen, W. R.** (**1914**). Biol. Bull. 27: 127; (**1921**) *ibid.* 40: 210.
193. **Phillips, R. A.** (**1915**). Irish Nat. 24: 137.
194. **Taylor, J. W.** (**1928**). Irish Nat. J. 2: 36.
195. **Tansley, A. G.** (**1911**). "Types of British vegetation," p. 192.

196. **Schroeder, W. L.** (**1929**). Naturalist, p. 402.
197. **Walton, C. L.** and **Jones, W. N.** (**1926**). Parasitology, 18: 144 and 363.
198. **Brown, F. J.** (**1926**). Parasitology, 18: 21; **Harper, W. F.** (**1929**) *ibid.* 21: 189; (**1930**) *ibid.* 22: 202; (**1931**) *ibid.* 23: 310; **Rees, G.** (**1931**) *ibid.* 23: 428; **Talbot, S. B.** (**1933**) *ibid.* 25: 518; **Hesse, A. J.** (**1923**) J. Helminth. 5: 227; **Rees, F. G.** (**1932**) Proc. Zool. Soc. Lond. p. 1; **Agersberg, H. P. K.** (**1924**) Quart. J. Micr. Sci. 68: 361; **Matheson, C.** (**1930**) Trans. Roy. Soc. Trop. Med. Hyg. 23: 421; **Price, H. F.** (**1931**) Amer. J. Hyg. 13: 685.
199. **Franca, C.** (**1922**). Trop. Dis. Bull. 19: 648; **Manson-Bahr, P.** and **Fairley, N. H.** (**1920**) Parasitology, 12: 50; **Fairley, N. H.** and **Jasudason, F.** (**1930**) Ind. Med. Res. Mem. p. 3.
200. **Matheson, R.** and **Hinman, E. H.** (**1928**). Amer. J. Hyg. 8: 279.
201. **Chandler, A. C.** (**1920**). J. Agric. Res. 20: 193; **Khalil, M.** (**1926**) J. State Med. 34: 472; **Walton, C. L.** and **Jones, W. N.** (**1925**) J. Min. Agric. 32: 186; (**1927**) *ibid.* 34: 734; **Ross, I. C.** and **McKay, A. C.** (**1929**) Comm. Australia Council S.I. Res. Bull. 43.
202. **Saunders, J. T.** (**1921**). Proc. Camb. Phil. Soc. 20: 351; (**1925**) "Natural history of Wicken Fen," p. 162.
203. **Coates, H.** (**1922**). J. Conch. 16: 319.
204. **Ellis, A. E.** (**1926**). J. Conch. 18: 52.
205. **Germain, L.** (**1925**). "La faune des lacs, des étangs et des marais," p. 209.
206. **Pantin, C. A. F.** (**1931**). J. Exp. Biol. 8: 63, 73 and 82; **Prutti, H. S.** (**1932**) Nature, 130, 312; **Ellis, W. G.** (**1933**) *ibid.* 132, 748.
207. **Colton, H. S.** (**1908**). Proc. Acad. Nat. Sc. Philad. 60: 410.
208. **Baily, J. L.**, **Pearl, R.** and **Winsor, C. P.** (**1933**). Biol. Gen. 9: 324.
209. **Jackson, J. W.** (**1915**). Lancs Cheshire Nat. 8: 41.
210. **Barnes, H. T.** and **T. C.** (**1932**). Nature, 129: 691; (**1933**) *ibid.* 132, 538; (**1934**) *ibid.* 133, 198.
211. **Bowell, E. W.** and **Bazeley, E. H.** (**1895**). Devonia, 1: 56.
212. **Atkins, W. R. G.** (**1923**). Parasitology, 15: 205.
213. **Ellis, M. N.** and **N. D.** (**1926**). Science, 64: 579.
214. **Tucker, M. E.** (**1928**). Biol. Bull. 54: 117.
215. **Sechaiya, R. V.** (**1927**). J. Bombay Nat. Hist. Soc. 32: 154.
216. **Baily, J. L.** (**1931**). Biol. Gen. 7: 407.
217. **Heathcote, W. H.** (**1907**). J. Conch. 12: 13.
218. **Dean, J. D.** (**1904**). J. Conch. 11: 15.
219. **Cross, W.** (**1892**). Naturalist, p. 329.
220. **Long, F. C.** (**1888**). Science Gossip, p. 281; (**1892**) Naturalist, p. 331.
221. **Roebuck, W. D.** (**1904**). Naturalist, p. 295.
222. **Peacock, E. A. W.** (**1905**). Naturalist, p. 240.
223. **Tye, G. S.** (**1875**). J. Conch. 1: 58.
224. **Nelson, W.** (**1883**). J. Conch. 4: 117.
225. **Alkins, W. E.** (**1921**). Mem. Proc. Manch. Lit. Phil. Soc. 65; (**1919**) J. Conch. 16: 119.
226. **Hurst, C. P.** (**1920**). Wilts Arch. Nat. Hist. Mag. 41: 149.
227. **Stubbs, A. G.** (**1900**). J. Conch. 9: 363.
228. **Walton, C. L.** (**1933**). Northw. Nat. 8: 326.
229. **Butcher, R. W.** (**1927**). J. Ecol. 15: 55; (**1933**) *ibid.* 21: 58.
230. **Kendall, C. E. Y.** (**1921**). J. Conch. 16: 244.
231. **Peacock, E. A. W.** (**1917**). Selborne Mag. 28: 80 and 97.
232. **Krull, W. H.** (**1931**). Occ. papers mus. zool. univ. Michigan, no. 226.
233. **Atkins, W. R. G.** and **Lebour, M. V.** (**1924**). Sci. Proc. Roy. Dub. Soc. 17: 327.
234. **Gardiner, J. S.** (**1928**). Natural history of Wicken Fen, p. 379.
235. **Butcher, R. W.** (**1924**). Naturalist, p. 175.
236. **Godwin, H.** (**1923**). J. Ecol. 11: 160.
237. **Webster, W. T.** (**1919**). Proc. Malac. Soc. 13: 85.
238. **Kennard, A. S.** and **Woodward, B. B.** (**1903**). Essex Nat. 13: 80; **Hardy. J. R.** (**1906**) J. Conch. 11: 273; **Standen, R.** (**1904**) *ibid.* 11: 83; (**1907**) *ibid.* 12: 19.

239. **Thomasson, M. W. (1912).** Trans. Caradoc Severn Valley F.C. 5: 237.
240. **Lefevre, G.** and **Curtis, W. C. (1912).** Bull. Bureau Fisheries, 30: 105.
241. **Stelfox, A. W. (1912).** Proc. Roy. Irish Acad. 31: 9.
242. **Boycott, A. E. (1896).** Science Gossip, 3: 114.
243. **Lowe, E. J. (1853).** "The conchology of Nottingham," p. 158.
244. **Lechmore, A. E. (1918).** J. Roy. Micr. Soc. p. 28.
245. **Henson, P. P. (1922–23).** Rep. Rugby Schools N.H. Soc. p. 23.
246. **Jeffreys, J. G. (1862).** "British Conchology," vol. 1; (**1869**) Supplement in vol. 5.
247. **Tate, R. (1866).** "A plain and easy account of the land and fresh-water mollusks of Great Britain."
248. **Oldham, C. (1930).** J. Conch. 19: 25.
249. **Borden, M. A. (1931).** J. Mar. Biol. Assoc. 17: 709.
250. **Mozley, A. (1932).** Amer. Nat. 66: 235.
251. **Evans, W. E. (1898).** Scot. Nat. p. 185.
252. **Houston, A. C. (1929).** Annual report Metropolitan Water Board.
253. **Whitehead, H. (1935).** J. Anim. Ecol. 4: 58.
254. **Forbes, E.** and **Hanley, S. (1853).** "British Mollusca," 4: 176.
255. **Coward, T. A. (1914).** Mem. Proc. Manch. Lit. Phil. Soc. 58: no. 9; **Ellis, A. E. (1933–34)** Trans. Norfolk Norwich Nat. Soc. 13: 451.
256. **Clark, H. W.** and **Wilson, C. B. (1912).** Bureau of Fisheries Document 757, p. 58.
257. **Bloomer, H. H. (1927).** Proc. Malac. Soc. 17: 208.
258. **Pearsall, W. H. (1925).** Naturalist, p. 278.
259. **Andrews, M. K. (1894).** Irish Nat. 3: 94; **H. P. V. (1935)** Countryman, 9: 504.
260. **Oldham, C. (1935).** J. Conch. 20: 161.
261. **André, E. (1893).** Rev. Suisse Zool. 1: 427.
262. **Shaw, W. A. (1904).** J. Northants N.H. Soc. 12: 218.
263. **Harrison, T. H.** and **Hurrell, H. G. (1933).** Proc. Zool. Soc. Lond. p. 207.
264. **Thompson, W. (1841).** Ann. Mag. Nat. Hist. 6: 121.
265. **Fordham, W. J. (1935).** Naturalist, p. 113.
266. **Stainforth, T. (1920).** Naturalist, p. 168.
267. **Nekrasov, D. N. (1926).** Russ. Hydrobiol. Zeit. 4: 184.
268. **Pelseneer, P. (1928).** Bull. Soc. Zool. France, 53: 158.
269. **Prashad, B. (1928).** Mem. Ind. Mus. 8: 157.
270. **Morehouse, E. M. (1931).** J. Conch. 19: 151.
271. **Richardson, H. (1887).** Nat. Hist. J. 11: 29.
272. **Hey, W. C. (1887).** Naturalist, p. 237.
273. **Boycott, A. E. (1929).** Proc. Malac. Soc. 18: 222.
274. **Pick, W. H. (1926).** "Elementary Meteorology," p. 21.
275. **Cockerell, S. C. (1887).** Naturalist, p. 190.
276. **Crowther, H. (1879).** Naturalist, p. 42.
277. **Crowther, H. (1894).** J. Conch. 7: 420.
278. **Welch, P. S. (1935).** "Limnology."
279. **Tattersall, W. M., Coward, T. A.** and **Mumford, E. M. (1914).** Mem. Proc. Manch. Lit. Phil. Soc. 58: no. 8.
280. **Ellis, A. E. (1924).** J. Conch. 17: 189.
281. **Shrubsole, G. (1935).** J. Conch. 20: 130.
282. **Murray, J.** and **Pullar, L. (1910).** "Bathymetrical survey of Scottish fresh-water lochs."
283. **Scott, T. (1890–99).** Eighth to seventeenth annual reports of the Fishery Board for Scotland: part III.
284. **West, G. (1905).** Proc. Roy. Soc. Edin. 25: 967; (**1910**) *ibid.* 30; 98; and in ref. 282.
285. **Richardson, L. (1935).** "Wells and springs of Herefordshire" (Geol. Survey).
286. **West, W.** and **G. S. (1909).** Proc. Roy. Soc. B, 81: 165.
287. **Standen, R.** and **Hardy, J. R. (1893).** J. Conch. 7: 266.
288. **Crampton, C. B. (1911).** "The vegetation of Caithness considered in relation to the geology"; (**1914**) "Geological survey memoir on Caithness."

289. **Wilson, G. V.** *et al.* (**1935**). "Geology of the Orkneys" (Geol. Survey).

290. **Morgan, I. B.** (**1887**). Collections historical and archaeological relating to Montgomeryshire: issued by the Powys-land club for the use of its members, 21: 103; (**1888**) *ibid.* 22: 231.

291. **Pearsall, W. H.** (**1920**). J. Ecol. 8: 163.

292. **Baillie, W.** (**1887**). J. Conch. 5: 192; (**1889**) *ibid.* 6: 15.

293. **Fox, H. M.** and **Simmonds, B. G.** (**1932**). Nature, 130: 277; (**1933**) J. Exp. Biol. 10: 67.

294. **Rimmer, R.** (**1880**). "Land and freshwater shells of the British Isles."

295. **Jackson, J. W.** (**1907**). J. Conch. 12: 54.

ADDENDA

p. 120. M. J. Longstaff (*J. Conch.* 13: 108) records 17 young in *Sphaerium lacustre*, and N. H. Odhner (*ibid.* 16: 219) 20 in *Pisidium hibernicum* and 16 in *P. obtusale*.

p. 122. An enemy which destroyed most of the snails in a locus each year without discriminating between different kinds might well delay or prevent the establishment of a new species which arrived in small numbers.

p. 128. W. E. Hoyle (*J. Conch.* 9: 109) notes *Limnaea glabra* with *L. stagnalis* and *L. peregra*.

p. 137. It may not be clear that "number of loci" in Table 1 means "number of loci containing *Pisidium* of some kind".

p. 147. *Limnaea peregra* and *Ancylus fluviatilis* occur in Ffynnon Lloer, N. Wales, at 2250 ft. (C. Oldham, *J. Conch.* 13: 353 add 15: 54) and *A. fluviatilis* in Ffynnon Frech at 2250 ft. (plate 4). W. D. Roebuck (*J. Conch.* 7. 367) records *Limnaea auricularia acuta* found by L. W. Hinxman at "1400 to 1600 ft." at Inchrory in Glenavon, Banff, but the locality seems very unlikely and elsewhere the species is essentially lowland.

p. 151. *Sphaerium corneum* occurs in L. Gwernan on Cader Idris (C. Oldham, *J. Conch.* 16: 287) which has calcium 5.

p. 160. S. G. Rich (*Science* 42: 579) describes *Unio complanatus* with a soft flexible shell from waters on granitic gneiss in New England.

p. 176. Without impugning Montagu's accuracy, it must be confessed that his canal "between Chippenham and Laycock" is, in nineteenth century terminology, the Wilts and Berks canal which makes a junction with the Thames at Abingdon.

NOTE

PEST OUTBREAK ENQUIRY

In a study dealing with the frequency, intensity and geographic distribution of areas periodically affected by insect and other outbreaks throughout the world, the problem of dealing with outbreaks either not recorded in the literature or in publications likely to be overlooked or not easily available has been encountered. The writer would appreciate, therefore, the calling to his attention of any outbreaks not recorded, or reported upon in obscure publications. He is most interested in outbreaks which have occurred at least twice in the same general area, and in as much as possible of the following information as may be available:

(1) The general area of outbreak.

(2) The date of first noted increase of the species, the height of infestation, and the time when it was last noted as a serious pest.

(3) Whether or not the species is normally present in smaller numbers or has invaded the infested area from another place.

(4) (If possible) whether the decrease in the infestation was due to parasitism or natural control, cultural control, or climatic influences.

Any information on this subject, which will be much appreciated, should be sent to

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REVIEWS

THE FEBRUARY ISSUE OF THE *JOURNAL OF ECOLOGY* (VOL. 24, NO. 1, FEBRUARY, 1936)

This number contains 12 original papers, notices of recent literature, an account of the Annual Meeting at Reading, the revised Constitution and Rules of the Society and the list of members. P. W. Richards published the first part of his observations on rainforest in Sarawak, on the lines of the earlier papers by T. A. Davis and himself on the Guiana rainforest. These careful analyses of the detailed structure of rainforest in widely separated regions of the tropics are of fundamental value. J. G. Myers writes of his reconnaissance journeys on the interior plateau of Guiana, an area little known botanically and whose vegetation has hitherto been undescribed.

Parts of two extended studies of East Anglian areas are H. Godwin's account of the establishment and development of Fen Scrub at Wicken Fen, and A. S. Watt's general consideration of the Climate, Soil and Vegetation of Breckland. Minor British studies are G. Philip's description of an enalid community (Zosteretum) in the Humber estuary, and Messrs Heddle and Ogg's account of irrigation or flushing experiments with spring water on a Scottish hill pasture, in which they record the raising of the *p*H value and the change to vegetation more palatable and nutritious to stock. W. Watson gives a useful account of the bryophytes and lichens of beechwoods, the late S. K. Mukerji contributes the first three sections of his extended study of the autecology of *Mercurialis perennis*, and Katherine Warington writes of the effect of temperature on the germination of weed seeds.

Of more theoretical papers there is A. R. Clapham's on statistical methods in the study of the distribution of individuals in vegetation, illustrated by an interesting analysis of "over-dispersion" in grassland; F. E. Clements's valuable account of the concept of "the climax" and its applications; and a short summary of "biotic community" terminology on the lines of Clements and Shelford, by J. R. Carpenter.

Reviews deal with the November issue of the *Journal of Animal Ecology*, and books and papers on wholesale erosion in America resulting from the misuse of land, on Swiss fens, on the Italian International Phytogeographical Excursion of 1934, on the heat economy of plants, etc.

A. G. TANSLEY.

A NEW INVADER

Nicolaus Peters and **Albert Panning**. *Die Chinesische Wollhandkrabbe* (Eriocheir sinensis *H. Milne-Edwards*) *in Deutschland*. Zoologischer Anzeiger, Supplement to Vol. 104, pp. 1–180. Leipzig, 1933. With Appendix by W. Schnakenbeck.

The Chinese mitten crab, already widespread in Europe, has reached the Thames. In 1935 one was caught alive in a water-screen at Chelsea. There may be others, and it may not be long before the occupation of British river systems by this new pest is in full swing. The crab gets its name from the very hairy appearance of the front claws.

The Ministry of Agriculture and Fisheries have already issued a warning leaflet (Fisheries Notice, No. 22), since various experts, and in particular Dr W. T. Calman of the British Museum of Natural History, had foreseen that this crab would inevitably spread here from Europe. Pycraft discusses the matter in an interesting popular article in *The Illustrated London News* for Dec. 14th, 1935, to which the general reader may be referred. For ecologists the important German monograph reviewed here comes at an opportune moment.

Its authors did their work at the Zoologisches Staatsinstitut, and the Zoologisches Museum in Hamburg, where important enquiries into the spread of the Chinese crab have also been done by Schnakenbeck.

The account begins in the traditional fashion with a long and detailed description by Panning, covering 55 pages, of the systematics, world distribution and structure of the crab. It is obviously of great value to have the synonymy of the species, and the distribution in Asia of allied forms, carefully traced. The structural details have one important use in checking any changes that may occur in the new countries of occupation. Ecologists will, however, find their main interest in the rest of the monograph in which Peters reviews the ecology, and economic significance of the crab.

The following are the main facts at present known about the mitten crab:

Original distribution. North China, down at least to Shanghai. Another species, *E. japonicus*, inhabits Japan and South China. It is not known if the ranges of these two overlap. They may only be geographical races occupying different climatic habitats. It is suggested that if the crabs spread farther south in Europe they may show structural changes in the warmer climate.

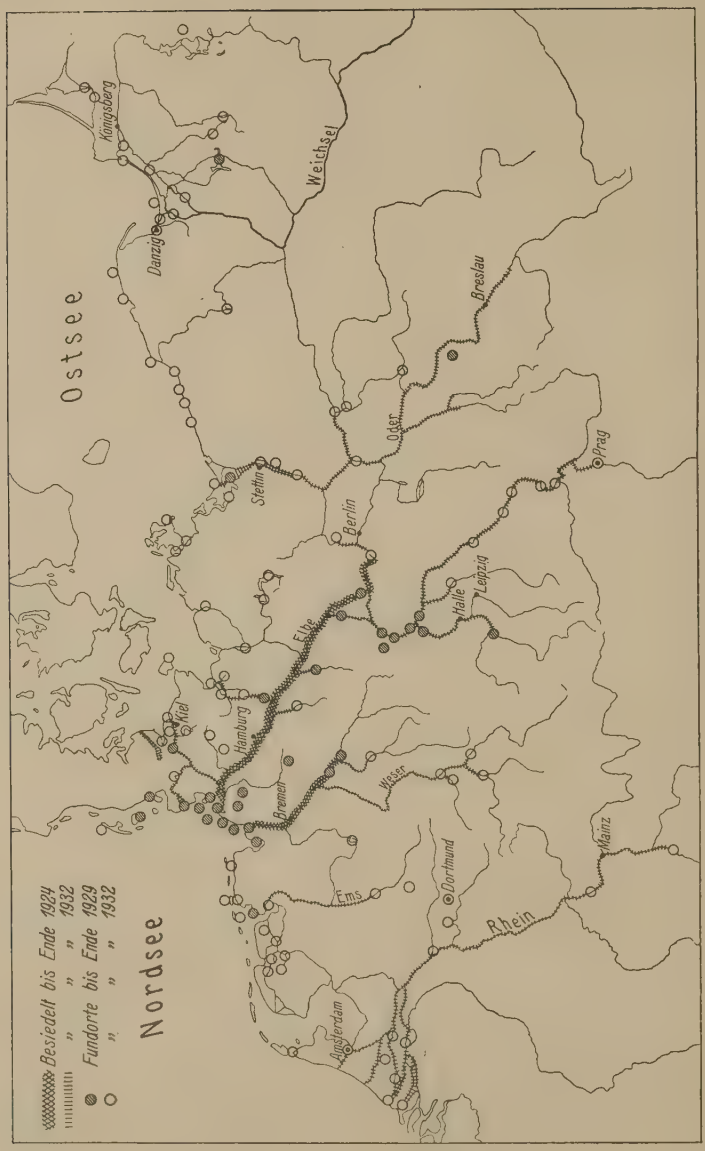
Sexes. Differ in the shape of the carapace and abdomen. Mature crabs weigh upwards of 50 gm.

Dispersal. Not definitely known how it got from China to Germany, but almost certainly either in marine growths on the bottoms of ships or in the sea water ballast tanks. Other cases are cited: two species of Indo-Pacific crabs have reached the Adriatic; various crabs have been found among marine growths on ships; another Chinese crab (*Pilumnoides perlatus*) has turned up on the Scilly Islands. The most important direct evidence is that in December 1932 a Hamburg-American steamer was found to have two large mitten crabs in the sea water ballast tanks: owing to the small size of the grill covering the seawater intakes these crabs must have got in when they were small and were almost certainly picked up in Hamburg Harbour. But it seems to us that the general use of small mesh grills makes it highly improbable that the crabs could get out of such ballast-tanks when they had been in them a few weeks and begun to grow up. *Arrival in Europe.* First found in a tributary of the Weser in September 1912. The history of the subsequent spread was mainly worked out by Schnakenbeck from Hamburg. During the War mitten crabs appeared in the Elbe. *Present distribution.* Nearly the whole of North Germany and Holland (see map), also in Belgium and along the Baltic coast beyond Konigsberg. It now occurs hundreds of miles from the sea and has penetrated up the Elbe as far as Czecho-Slovakia, at Prague. It occurs in the Oder beyond Breslau, in the Rhine beyond Mainz and in the Ems. It is also found in the Weser and Wechsel.

Habitat. The bottoms and banks of fresh waters and estuaries. This is the normal habitat which is left only when the crabs migrate to the lower estuaries and sea to breed. They live both in standing and running water. They occasionally come up on land and frequently live in intertidal regions. They can stand quite oily water, but the authors do not say much about the effects of other pollution. *Physiology.* Can withstand high variations in salinity, and can live out of water for about a week. *Hibernation.* In winter, when the old sexually ripe crabs migrate to the coast, the small and medium sized ones remain inland, mostly moving down into the deeper water.

Food. Omnivorous, but details not fully known. Includes netted and dead fish, Crustacea, insects (especially larvae of *Chironomus*), molluscs, worms, and each other. They avoid frogs and newts. They eat water plants such as *Potamogeton, Elodea,* duckweed (*Lemna*) and filamentous Algae. They have a taste for soft animals such as snails and bivalves. There is no case known of mitten crabs catching and eating live fish, but they may possibly go for spawn. *Habits.* Feed mainly at night, but are also active during the day; in winter they are active, and the gut is often full of food. The mitten crab can go without food for at least a month.

Burrows. The fishermen of the Lower Elbe, engaged in eel trapping at night, discovered that what had appeared to be rat runs were made by mitten crabs. In the right kind of soil, there may be as many as 30 burrows in a square metre. These are most conspicuous



Distribution of mitten crab in Europe up to the end of 1932.

in intertidal stretches. They are usually about 4–5 cm. wide and 40–60 cm. long. They cause serious damage to the banks.

Migration and breeding. Essentially a marine animal which returns to the sea to breed, like the eel. The direction of migration is not necessarily controlled by the flow of water, although this speeds it up, since crabs living in stagnant water also perform the migration. The planktonic *Zoaea* larvae have not yet been detected in nature. The *Megalopa* larvae migrate inland by swimming. The movements of the later stages are better known. They are most strongly marked in spring and have helped to spread the crab 440 miles up the Elbe and over 800 miles up the Yang Tse Kiang. The downward movement, which is among

The spawning area of the mitten crab at the mouth of the Elbe.

animals over 40 mm. long, takes place in autumn and winter and mostly in mid-stream. The sex ratios indicate that the males move much farther up-stream than the females and that the latter tend to stay in the estuaries, and lower parts of the river.

Both in nature and in captivity breeding takes place only in brackish and sea water. Pairing activity may occur in fresh water, but the eggs are not laid. They breed over a longish period from about November to July, when both sexes swarm in thousands in the brackish water estuaries. Females go farther out to sea, with the eggs carried on the hairs of the pleopods from which they hatch as larvae (see map, above). One female crab produces from several hundred thousand to a million eggs at one laying. The crabs stay for some time at sea or in the estuaries, and often get completely covered with marine growths.

Growth and length of life. They grow only during the warm months, mainly June–

September. Sexual maturity is probably reached between the fourth and sixth years when the length is over 45 mm. Statistics suggest that few survive to breed after their fifth year, although occasionally big crabs occur which may be as much as ten years old.

Damage. Erosion of banks has already been mentioned. They are also a pest to fisheries: eating the bait off lines (especially eel lines), destroying nets, taking up valuable space in the nets, eating netted fish, bruising the fish when the nets are pulled in and reducing potential fish food. Two fishermen in the Lower Elbe had their nets so full of mitten crabs that they could not lift them out of the water: there was probably half a ton of crabs.

Control. Quite impossible at present and perhaps always. There are natural enemies, among which brown rats may be important. Fish eat mitten crabs, e.g. the eel, burbot, cod, trout, perch and pike. No natural epidemics have yet been observed, while experimental diseases might be dangerous to crayfish and fish. The only possibility seems to be for fishermen to catch the breeding females. Mitten crabs are still spreading, and apparently increasing in some of their older centres of occupation.

Value. Although edible to man and animals and chemically valuable, little use has been made of them. They are rather too small for human consumption, but pigs certainly like them. They also make good bait for eels.

Schnakenbeck contributes an Appendix on crab larvae. There is a large bibliography with 168 references, and the monograph is fully illustrated by text-figures and photographs. I am greatly indebted to the Akademische Verlagsgesellschaft, Leipzig, for permission to reproduce in this review two of the excellent maps.

One misses any serious attempt to assess the density of crab populations at different times and places: this is of particular importance, since the present estimates of abundance and of increase and decrease are based only on the impressions of observers from what they see and catch. The history of this sudden spread is impressive and will no doubt be repeated again and again by other species in the future. It teaches us that (as in the case of the cord grass, *Spartina townsendii*) there are many ecological niches still to be filled by well-equipped invaders.

The mitten crab will no doubt join the growing band of invaders to this country, which already includes the grey squirrel, muskrat, French partridge, little owl, willow grouse, rainbow trout, black bass, Continental crayfish, American slipper-limpet, and several oyster-tingles; not to mention a host of insects, among which the most distinguished recent visitor is the Colorado potato beetle. There seems no reason to suppose that this list will not continue to grow, even though the folly of deliberate introductions is prevented.

In the present instance, we are fortunate in having such a competent study of the mitten crab's ecology ready to hand before the invasion has got under way. So far as one can see, the only factor likely to limit its establishment in the British Isles would be a zone of chemical pollution in the estuaries. Whether this will ever be deliberately planned depends upon the extent to which fresh-water fishermen are able to influence Government action.

CHARLES ELTON.

THE ECOLOGY OF MARINE COASTS AND ESTUARIES

(1) **V. E. Shelford, A. O. Weese, Lucile A. Rice, D. I. Rasmussen, Archie MacLean, Nettie M. Wismer,** and **John H. Swanson.** *Some marine biotic communities of the Pacific coast of North America.* Ecological Monographs, 5: 250–354, 1935. 20 tables, 14 figures and maps.

(2) **G. E. MacGinitie.** *Ecological aspects of a California marine estuary.* American Midland Naturalist, 16: 629–765, 1935. 3 maps, 21 figures.

(3) **W. B. Alexander, B. A. Southgate** and **R. Bassindale.** *Survey of the River Tees. Part II: The Estuary—Chemical and biological.* Department of Scientific and Industrial Research, Water Pollution Research, Technical Paper No. 5. xiv+171 pp., 117 tables, 65 figures, 2 maps. (H.M. Stationery Office, London, 1935. Price 9*s.* 0*d.* net, postage extra.)

(**1**) The principal marine climax communities in the area of the former Puget Sound Biological Station (now Univ. of Washington Oceanographic Laboratories) near Vancouver Island which are associated with the bottom are bivalve-annelid communities (the *Pandora-Yoldia* and *Macoma-Paphia* biomes) and gastropod-barnacle communities (the *Strongylocentrotus-Argobuccinum* and *Balanus-Littorina* biomes). The studies were made during the years 1926–30 and are essentially an expansion and continuation of those begun by Shelford and Tower in 1922.[1] A description of each of the biomes is presented in varying detail with discussions on their component fasciations and associations. In certain instances reference is made to ecological studies done in the laboratory with characteristic animals in the communities, and in all emphasis is laid upon the abundance of the different forms at the various collecting stations.

Two of the communities are characteristically subtidal: the *Strongylocentrotus-Argobuccinum* biome, which is associated with relatively swift moving water, high salinity, high light penetration, and little plankton; and the *Pandora-Yoldia* biome with relatively slower moving water, lower salinity, slow fine silt deposition, and much bottom detritus. These two communities are apparently restricted to the North Pacific, although communities similar to the former (composed, however, of different species) exist at Vineyard Sound and to the latter at Buzzard's Bay (both Southern Massachusetts) and near Denmark.

The *Macoma-Paphia* biome is essentially subtidal, although it may be exposed in its upper reaches at low tide; its most characteristic form is the edible clam. While resembling a general type found throughout the Northern Hemisphere at least, it cannot be said to compare precisely with any other community thus far described. The *Balanus-Littorina* biome is a true "tidal" (i.e. intertidal) community and is largely determined by water movement; it is characterised by barnacles epizootic upon mussels. Examples of the community were studied in this region (Rice) and in southern California near La Jolla (Rasmussen). This general type of community was considered as being characteristic of many shores in both the Atlantic and Pacific in the Northern Hemisphere.

The investigation dealt chiefly with bottom communities; but throughout the whole the influence of the above pelagic communities and their constituents are emphasised. Also, there are studies dealing with succession in the ecotone between the *Strongylocentrotus-Argobuccinum* and *Pandora-Yoldia* biomes in relation to the physiographic processes taking place there, in the early and late stages toward land, in which *Salicornia* plays an important part (Weese, MacLean, Markus). In a detailed study of a series of stations at the edge of "Brown Island" (Swanson and Wismer) it was shown that the maximum number of animals occurred in subtidal areas.

"The writers are convinced that organisms, or more especially community groupings of organisms, are the best indicators of hydrographic conditions and that the success or failure, presence or absence, scarcity or abundance of these living things is correlated with determinable physical and chemical conditions. To yield best results, the study of (environmental) conditions and of communities must go hand in hand, but also the nature of the study of conditions must constantly be moulded by a study of the correlation of the responses of organisms with the knowledge of conditions already gained."

This paper is an important contribution both to the knowledge of marine communities of the region studied and to the understanding of community composition, structure, development, and local distribution of dominance: all important principles of ecology making the paper doubly valuable. Although not so stated this monograph is a summary

[1] 1925, Pub. Puget Sd. Biol. Sta. 5: 33–73.

of the work done at the Puget Sound Station before the regrettable change of policy which precludes the continuation there of ecological studies on a community basis.

(2) This is an account of general ecological studies made at Elkhorn Slough, a tributary of Monterry Bay, California, in the years 1926–35. It includes a physiographic history of the slough, and the changes which took place during the eight years of study. The physiographic inconstancy of the habitat from year to year (and frequently from tide to tide) made it seem inadvisable to take the findings from any community basis or successional viewpoint, notes on the associates of any given species being relegated to the discussion of individual species.

There is, however, a discussion on the food chain relationships of the slough as a whole (i.e. for the local complex of communities within the slough) and figures for weights are presented which illustrate very well the concept of the "pyramid of numbers": each link in the food chain is said to be one-tenth of the link preceding it. In a pelagic chain 10,000 lb. of Algae go to support 1000 lb. of small Crustacea, which in turn feed 100 lb. of small fish which are eaten by 10 lb. of large fish which (when carried to the homocentric conclusion) feed 1 lb. of man. Attention is called to the important role of bacteria in converting the food supply of the plants (chiefly *Zostera*, *Enteromorpha*, *Polysiphonia* and miscellaneous drifting Algae) into detritus available for bottom feeders. In such a food chain 10,000 lb. of plant make 1000 lb. of detritus, which feeds 100 lb. of clams or mudshrimps; the latter are fed upon by stinging rays, birds and man. But no data are given to substantiate the exact weights of the various portions of the food chains.

Collections were made at eight stations in the slough and while no quantitative data are presented the latter two-thirds of the paper is devoted to a number of autecological notations on the individual species which are arranged as a phyletic list. Included also are discussions on collecting apparatus, influences of the tide, nocturnal activity, and a plea for more intensive work in the field from an ecological viewpoint.

It is to be regretted that no attempt was made in this paper to formulate even a tentative system of communities, and that there was a complete lack of quantitative data about the collections. The specific notes on the habits and food relationships make the paper a valuable one to ecology, the utility of which would have been enhanced by presenting the autecological notes in an outline similar to his brief food-cycle discussion rather than in the taxonomic catalogue system used.

(3) The influence of industrial and sewage pollution upon the biota of inland streams has proved in the past an attractive study for many workers in applied ecology; this paper is an attempt to discover the effects of sewage and industrial wastes upon the biota of a marine estuary. As a representative river receiving such pollutions the River Tees (South Durham), which for 25 miles from the sea preserves a tidal section, was selected. The whole body of water in the estuary throughout this section moves to and fro with the tides. Salt water is found at normal low tides as far as 11 miles from the sea, and at high tides from 14 to 15 miles, depending on the time of year. A decided stratification of the river is found with respect to salt content, the salt (in parts per thousand by weight) being greater at the bottom of the river than at its surface.

To check observations and to observe the actual results of pollution, data for the estuaries of the Tay and of the Tamar[1] were compared with those of the Tees. Both the Tees and the Tay are swift flowing rivers subjected to peat floods, are of similar salinity, and since both discharge into the North Sea it was considered that they should possess a similar biota. It was found (using *presence* or *absence* of species as a criterion, i.e., using the number of *species*, not *individuals*, present) that there was little general difference in faunal distribution between the two streams: a large number of species occurred both in the fresh water and salt water extremes of the rivers, a lesser number being in the middle area.

It was shown that the distribution of species in marine estuaries is controlled by interaction of a number of factors, oxygen content not being necessarily an important one,

[1] Tamar data from **Percival**, 1929, J. Mar. Biol. Ass. U.K., 16: 81.

variability in salinity (from tide to tide) a more important but by no means a controlling factor, and the type of bottom probably the deciding factor, at least locally. It is to the latter item that the differences in species distribution (invertebrate) in the Tees, Tay, and Tamar estuaries are attributed. In analysing the data and comparing the species distribution with these environmental factors, an interesting series of graphs are used, including those showing the distribution of species in a transect of the rivers, species common to two or all of the streams (although species lists are not included), to the method of feeding (suspension or non-suspension), to the type of bottom selected by the bottom living species, and tidal *versus* bottom species. In sand and mud areas the salinity conditions appear to be more stable, and the range of burrowing marine species (as compared with the non-burrowing forms) is locally increased there.

In laboratory experiments it was found that of the two main poisons included in the industrial pollution, cyanides were far more important in their discharged concentrations than were the tar acids, although the latter were, by weight, two and a half times more abundant. General toxicity was found to be increased by a lowering of dissolved oxygen. Of six crustaceans experimented upon, only two (*Crangon vulgaris* and *Praunus flexuosus*) were apparently affected by the cyanide. Experiments conducted with rainbow trout (*Salmo viridescens*) indicated that the deaths of this form which take place during the May migratory season are very evidently caused by cyanide poisoning. The lethal effects are reflected in the marked decrease of the salmon and trout fisheries in the Tees which began in 1913 and resulted in the practical extinction of the estuary fisheries by 1928.

Data are presented dealing with the degree of oxygen demand by the pollutions and their rate of absorption. It was found that tar acids (which are here innocuous to life) may be removed by the addition of sewage, which accelerates the decomposition of the former. Sewage has little effect on the cyanide absorption, but the mixing of local waste products containing ferrous chloride converts the poison into ferrous cyanide which renders it innocuous. Modification of the existing coke apparatus in use on the Tees to reduce tar discharge was not considered practicable at present.

It would seem that the work with the bottom fauna would have been much more satisfactory had quantitative data of the forms been used rather than mere species lists, for in this way the difficulties experienced in comparing the fauna of a river of sand, mud, and rock bottoms with one of only sand and mud would have been facilitated. There has been no attempt in the study to correlate individual species with either communities or habitats: distances from the sea, oxygen content, and degrees of variability of salinity alone have been used. The application of the principles of community ecology would, therefore, have made this paper much more valuable both as a scientific contribution, and in its essential purpose—the discovering of the effect of pollution in the estuary. Concise summaries at the end of each of the rather involved and somewhat disconnected chapters as well as a consolidated bibliography would also have proved useful.

Each of the papers reviewed has a brief discussion on collecting methods and apparatus.

J. RICHARD CARPENTER.

THE GEOGRAPHICAL DISTRIBUTION OF ANIMALS

Zoogeographica: International Review for Comparative and Causal Geography. Edited by **Fridthjof Ôkland**, in collaboration with **Sven Ekman** and **Richard Hesse**. Gustav Fischer, Jena, Germany. Vol. 1 (1932–3, pp. 1-608); vol. 2 (1933–5, pp. 1–634); vol. 3 (1935 onwards). Price varies.

Zoologists have often felt the extreme need in recent years for monographs in which the earlier work on geographical distribution, e.g. the classical works of A. R. Wallace, could receive careful revision in the light of later discoveries. *Zoogeographica* was started in 1932

and has during the first few years of its existence signally succeeded in fulfilling this need. It is not possible to cite in detail the 41 articles which have already appeared in it.

There has grown up in the last 20 years a school of animal geographers, especially in Scandinavia, the Baltic, and Germany, who have been undertaking a thorough overhaul of earlier work. One of the most striking features of this later work is the extent to which fossil records are now becoming available for the elucidation of problems which were the subject of purely arm-chair speculation in the last century. Another is the growing completeness of marine animal records, enabling reliable maps of their distribution to be made. The ecological aspects are also treated in this journal, and are considered as one of the means of reconstructing the past.

The following list of subjects will give some idea of the scope and importance of *Zoogeographica*, which should be in the possession of every large zoological library (it is, I believe, taken at present by only two in this country): the distribution of animals in relation to the Ice Age—cave animals, *Diaptomus*, Alpine fauna, birds; the fauna of Labrador, Cyrenaica, islands in the Baltic, of Lake Baikal in Siberia; butterfly faunas of Palestine, South Arabia; fresh-water fishes of Europe; the migration and distribution of eels; fresh-water flatworms of the Alps, and of the Balkans; the zoogeographical history of the southern continents, of bipolar species, of sea plankton; the relations between the Pacific and Atlantic faunas and their history; British-Scandinavian beetles; climatic changes and faunal evolution in Africa; fresh-water molluscs in Russia and land planarians in Germany; the ecology of littoral marine animals on a Baltic island, of the liver fluke in Norway; and others.

It is to be hoped that the journal will be able to flourish, and also that it may be able to continue some of the literature abstracts which appeared in 1933 and 1934.

CHARLES ELTON.

SHORT REVIEWS

Lilian J. Clarke. *Botany as an experimental science in laboratory and garden.* Oxford University Press. London: Humphrey Milford, 1935. Pp. 1–138. Price 6*s*.

Dr Clarke did striking pioneer work in creating a system of teaching plant ecology at the James Allen Girls' School, Dulwich, by means of field plots representing different plant habitats and associations, combined with ingenious but simple laboratory experiments. Animal ecologists will find in these collected notes a good many useful ideas for research techniques, while teachers should find them invaluable in planning their own methods. The attitude of mind revealed is refreshing and compels thought about the possibilities of ecology teaching in schools.

J. W. Bews. *Human ecology.* Oxford University Press. London: Humphrey Milford, 1935. Pp. 1–312. Price 15*s*.

The key-note of this book is summed up by General Smuts in his introduction: "The world is not a chaos, a chance selection of items and fragments. It is a closely interwoven system of patterns." That ecology has much to contribute to human life is already clear. Bews has made the bold attempt of treating the whole range of human affairs as an ecological problem, and brings into his study facts from geography, anthropology, psychology, and cultural history—an attempt which is favoured by his experience of the racial and environmental background of South Africa. Although much material has been assembled by him, there is rather a lack of any impressive theory to bind the facts together. But the objective attitude of mind and the setting up of some framework in which research on human ecology can be planned, are of considerable value.

A. S. Pearse. *The migration of animals from sea to land.* Duke University Press, Durham, North Carolina, U.S.A., 1936. Pp. 1–174. Price 3 dollars.

This small book contains about 700 literature references, which constitute its chief value. It discusses the origin of life, various routes from the sea to land, the circumstances in which animals are likely to have made this important change in their method of life, and the changes in them after they have done so. Statements such as "Plants and animals cannot exist except in an environment" might have been omitted, and the conclusions of other workers treated in a rather more critical manner. But the advantage of having all the possibilities set out for discussion makes the book useful.

Walter P. Taylor. *Ecology and life history of the porcupine* (Erethizon epixanthum) *as related to the forests of Arizona and the South-western United States.* University of Arizona Bulletin, Vol. 6, No. 5, pp. 1–177. University of Arizona, Tucson, Arizona, U.S.A. Price 1 dollar.

This is one of the most complete studies of a single species of wild mammal that we have yet seen. The habits, distribution, food, breeding, enemies, parasites, psychology, migrations and other ecological matters are skilfully handled. The central economic importance of the porcupine in the United States is its damage to forest trees. The work covered the years 1922–7 and showed the wide extent of the problem. The author emphasises the necessity for ecological studies in each area before control measures are undertaken. A very interesting monograph and well illustrated.

R. G. Stapledon. *The land: now and tomorrow.* Faber and Faber, Ltd., 24 Russell Square, London, W.C. Pp. 1–336. Price 15*s.*

Agricultural land in this country is being converted to other uses at the rate of about 31,000 acres per annum. One of the author's tenets is that the country must in part be used for extended amenities for townspeople, so that the main theme of his book is the problem of improving the remaining land to produce higher returns, and of using the large area of waste or marginal land in a productive manner. His demonstration (including some very careful costing experiments) of the ways in which rough hill grazings, and in fact anything but the best pastures, can be improved by applying mineral salts and using modern grazing techniques is impressive. While giving full scientific attention to these problems and their corollaries, the book is at the same time animated by a furious idealism about preserving the land and enjoying the country, which commands respect. At the end a scheme for a large national park in the Welsh Hills is set forth. The whole book should be read by ecologists as it deals with a subject which is at the root of many national economic problems, while at the same time it covers a wide sweep of interlocked subjects. The discussion of hill grassland ecology is of direct value also to working ecologists.

Reginald L. Hine and Others. *The natural history of the Hitchin Region.* Hitchin and District Regional Survey Association, 1934. Pp. 1–256. Price 7*s.* 6*d.*

This volume, by eight contributors, is lavishly produced and contains a number of articles on different subjects such as history, geology, meteorology, botany (aromatic and medicinal herbs), on various groups of animals, and on archaeology. The animals occupy about three-quarters of the book. Although a great deal of the matter consists of lists with various comments, there are many useful records and observations, some of which are of more than regional interest. A pocket at the end contains part of the one-inch Ordnance

Survey map, together with a chart giving twelve transects of the area in which the geology, vegetation, and human activities are summarised. There are a number of good illustrations and photographs, and an index.

Bodenheimer, F. S. *Animal life in Palestine: an introduction to the problems of animal ecology and zoogeography.* L. Mayer, P.O.B. 932, Jerusalem, Palestine, 1935. Pp. 1–506. Price £1. 7*s.* 6*d.*

This is an important and comprehensive study of the fauna of Palestine, complete with literature references, and lavishly illustrated by text-figures depicting a great many of the animals. It is clearly essential for anyone studying the Near East fauna. It is also of great value for general zoogeographical purposes. The significance of the subtitle (which is slightly misleading, as the book is not a general text-book of ecology) is in the way the author approaches his descriptions of the fauna. At every point he discusses the animals in relation to their environment, and with an eye to illustrating some general problem in ecology. Special mention should be made of the diagrams of seasonal occurrence and activity of different forms. The methods by which these figures were obtained are not given in detail. The book includes land, fresh-water and marine animals, and discusses several economic problems such as insect and vole pests, and the fisheries. This book is to be recommended in view of its wide scope and original approach.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

The entomological journals have been abstracted by H. F. Barnes and B. M. Hobby; the others by J. R. Carpenter, D. H. Chitty, Charles Elton and A. D. Middleton.

This series of notices covers most of the significant work dealing with animal ecology published in British journals, large and small. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, University Museum, Oxford.

Copies of these abstracts, on gummed paper, cut down to a width suitable for five-inch index cards, are issued free with the *Journal*. They can also be obtained separately by non-subscribers, from the Cambridge University Press, Fetter Lane, E.C. 4, or through a bookseller, price 3*s*. 6*d*. per annum, post free (about 300 notices, in two sets, May and November).

1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS

1. Omer-Cooper, J. and **Rawson, J. H.** (**1934**). "Notes on the British Sphaeromatidae (Crustacea, Isopoda)." Rep. Dove Mar. Lab. Ser. **3**, No. 2: 22–58.

A well-illustrated systematic account of these marine and brackish-water Isopods, with a full bibliography.

2. Fletcher, T. B. (**1935**). "List of species of micro-Lepidoptera added to the British list since the publication of Meyrick's Revised Handbook." Ent. Rec. 47: 112–14.

A list of 28 species with references.

3. Anon. (**1935**). "Microlarvae in the winter months." Ent. Rec. 47: 127.

Instructions for collectors of micro-Lepidoptera.

4. Thompson, G. B. (**1935**). "Notes on Mallophaga. III." Ann. Mag. Nat. Hist. 16: 214–17.

Reviews systematics and hosts of British species of *Philopterus* parasitic on Corvidae.

2. ECOLOGICAL SURVEYS AND HABITAT NOTES

(*a*) Marine

See also **53, 56**

5. Nichol, E. A. T. (**1935**). "The ecology of a salt marsh." J. Mar. Biol. Ass. U.K. 20: 203–61.

An important ecological survey of the biota and environmental conditions of various habitats in a salt marsh near Aberlady Bay on the south shore of the Firth of Forth. Seasonal movements of organisms from the adjoining marine and fresh-water areas are discussed, salinity playing an important part in regulating the fauna. There is also a brief discussion of the physiology of brackish-water organisms.

6. Nicholls, A. G. (**1935**). "Copepods from the interstitial fauna of a sandy beach." J. Mar. Biol. Ass. U.K. 20: 379–405.

"Interstitial fauna" refers to animals such as copepods, nematodes, rotifers, and Protozoa living in the capillary water which is held in sand even at low tide.

7. Pyefinch, K. A. (**1936**). "Habitat of *Procerodes* (*Gunda*) *ulvae*." Nature, 137: 32.

Observations made on Bardsey Island, North Wales, suggest that this flatworm occurs in certain types of shore material—moderate-sized stones over shingle; also that it moves about with local changes in salinity.

8. O'Donoghue, C. H. (1935). "Bryozoa encrusting the hairy porcelain crab." Ann. Mag. Nat. Hist. 16: 390–2.

Identifies the species found (see **9**).

9. Renouf, L. P. W. (1935). "Faunistic notes from the coast of Co. Cork, I.F.S." Ann. Mag. Nat. Hist. 16: 212–14.

Encrusting Bryozoa on the crab *Porcellana platycheles*. Unusual abundance of the Acinetarian *Ephelota* in Lough Ine during spring of 1935.

10. Renn, C. E. (1935). "A Mycetozoan parasite of *Zostera marina*." Nature, 135: 544–5.

Experimental proof that this parasite attacks *Zostera*. It occurs on both sides of the Atlantic.

11. Russell, F. S. (1935). "On the value of certain plankton animals as indicators of water movements in the English Channel and North Sea." J. Mar. Biol. Ass. U.K. 20: 309–32.

Certain species form reliable indicators of different types of water, e.g. *Sagitta setosa* as a North Sea element, and *S. elegans* as an Atlantic element.

(*b*) Fresh-water

See also **5, 138**

12. Anon. (1935). "Marshes and reed-beds in July and early August." Ent. Rec. 47: 90–1.

Very useful collecting notes for anyone wishing to breed Lepidoptera associated with such habitats.

(*c*) Land

13. Peacock, A. D., Smith, E. P. and **Davidson, C. F. (1935).** "The natural history of South Rona. Lepidoptera (by **J. W. Heslop Harrison**)." Scottish Nat. 31–4.

Lists with very few habitat notes.

14. Peacock, A. D., Smith, E. P. and **Davidson, C. F. (1935).** "The natural history of South Rona. Psyllidae (by **G. Heslop Harrison**)." Scottish Nat. 57–60.

Notes on species including their habitats. Also a list of dragonflies.

15. Massee, A. M. and **Thomas, F. J. D. (1935).** "The fauna of the weevil 'sack-band'. II." Ann. Mag. Nat. Hist. 16: 350–4.

Lists of insects collected from corrugated cardboard bands placed round apple trees.

16. Hey, G. L. (1935). "Notes on Capsidae." Ent. Mon. Mag. 71: 237–8.

The apple Capsid, *Plesiocoris rugicollis* F., as the predominating Capsid on black currant: not *Lygus pabulinus* L.

17. Williams, C. B. and **Killington, F. J. (1935).** "Hemerobiidae and Chrysopidae (Neur.) in a light trap at Rothamsted Experimental Station." Trans. Soc. British Ent. 2: 145–50.

Records the lacewing flies obtained in a light-trap fitted with a clockwork mechanism which changes the killing-bottles at regular intervals during the night, so that the approximate time of entry of the insects can be estimated. Contrary to the general rule for most groups of insects, the majority of specimens attracted to the light were females; while there is an indication that the green lacewings came to the trap later in the night and the brown lacewings earlier.

18. Killington, F. J. (1935). "Notes on the habitat and life-history of *Nathanica* (*Nothochrysa*) *fulviceps* (Steph.) (Neuropt.)." J. Soc. Brit. Ent. 7: 110–13.

The natural habitat of this extremely rare green lacewing in the imaginal, and possibly the larval stages, is the upper branches of oaks, and it may be on this account that so few examples have hitherto been taken: its rarity being more apparent than real.

19. Benson, R. B. (1935). "The alien element in the British sawfly fauna." Ann. Appl. Biol. 22: 754–68.

A discussion based largely on plant classification.

20. China, W. E. (1935). "A North American Jassid (Homoptera) in Surrey." Ent. Mon. Mag. 71: 277–9.

Graphocephala coccinea Forster on *Rhododendron*.

21. Syms, E. E. (1935). "Notes on the biology of *Microdon eggeri* Mik. (Dipt., Syrphidae)." Trans. Soc. British Ent. 2: 163–5.

This fly probably oviposits at the entrances to ants' nests. The young larvae are active, but the older ones more slug-like in shape and movement. The larva feeds on the solid food ejected from the hypopharyngeal pockets of the ants. Pupation takes place in the upper and drier parts of the nest. Larvae and puparia of *M. eggeri* were obtained from nests of *Acanthomyops niger* in standing stumps of pine in a damp meadow, Byfleet, Surrey.

22. Anon. (1935). "Some micro-larvae for the end of September and October." Ent. Rec. 47: 103.

Indicates many species of leaf-mining caterpillars to be found at this time of year.

23. Craufurd-Benson, H. J. (1935). "*Trigonogenius globulus* in 'Argol'." Ent. Mon. Mag. 71: 184.

A previous record of this breeding habit of *T. globulus* was published in **Scott, H.** 1921, Bull. Ent. Res. 12: 133–4.

24. Gambles, R. M. (1935). "Scottish Psocoptera." Scottish Nat. 83–8.

25. Bagnall, R. S. (1935). "Random notes on springtails (Collembola) in the north of England. I." Vasculum, 21: 98–103.

Distributional and systematic notes with descriptions of new species and references.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **5, 7, 17, 84, 92, 104, 108, 118, 126, 139**

26. Clark, J. E., Margary, I. D. and **Cave, C. J. P. (1935).** "Report on the phenological observations in the British Isles from December, 1933, to November, 1934." Quart. J. R. Met. Soc. 61: 231–84.

Reports from 518 stations summarised on maps showing isotherms, flowering dates of twelve species of plants, arrival dates of 20 species of birds, also departure dates of several species.

27. Alexander, H. G. (1935). "A chart of bird song." British Birds, 29: 190–8.

An important summary showing the months in which 98 species sing.

28. Frohawk, F. W. (1935). "Martins and wasps nesting together." Proc. R. Ent. Soc. Lond. 10: 71–4.

The two nests were built side by side under the gable of a house. This occurrence indicates a condition of mutual tolerance available for conversion by natural selection into a constant and normal association (cf. **J. G. Myers**, 1935, Trans. R. Ent. Soc. Lond. 83: 11).

29. Bull, H. O. (1935). "Studies on conditioned responses in fishes: Part III. Wave-length discrimination in *Blennius pholis* L." J. Mar. Biol. Ass. U.K. 20: 347–64.

Experiments in which blennies learned to make certain movements by associating different colours with electric shocks. This fish seems to have a wide range of colour vision.

30. Bull, H. O. (1935). "Studies on conditioned responses in fishes: Part IV. On the controlling influence of normal behaviour traits upon capacity to form experimental conditioned motor responses under certain conditions." J. Mar. Biol. Ass. U.K. 20: 365–70.

Pleuronectids are unable to form conditional motor responses after at least 200 trials, whilst other fishes have done so in less than forty.

31. Walton, G. A. (1935). "Field experiments on the flight of *Notonecta maculata* Fabr. (Hemipt.)." Trans. Soc. British Ent. 2: 137–43.

Concludes: (1) water is found by sight; (2) this sense is well-developed and the bugs can appreciate the difference between habitable water and (*a*) a light road, (*b*) glasshouses and (*c*) a thin layer of water over grass, and over soil. They have also detected such a small area of water as a water butt when surrounded by glasshouses, but were deceived by a black saloon car; (3) "When there is no other attraction the greater number of bugs will either (*a*) fly to the compass point of greatest illumination or (*b*) fly down wind, i.e. the line of least resistance."

32. Latter, O. H. (1935). "A reason for the order in which the queen wasp constructs the cells of the comb; a method for computing the number of cells in a comb, and an instance of the limitation of the instincts of wasps." Proc. R. Ent. Soc. Lond. 10: 74–8.

The order in which new cells are constructed depends upon the presence of a good foothold, i.e. two existing walls as a base. The total number of cells is estimated by summing an arithmetical progression whose first term is 4, common difference 6, and number of terms equal to the number of concentric rings of cells. In the case of a nest opened up by a badger the comb was completely destroyed; the queen was unable to resume her earlier function of comb-foundress, nor were the workers able to start a comb on their own without a base made by the queen.

33. Carpenter, G. D. H. (1935). "Courtship and allied problems in insects." Trans. Soc. British Ent. 2: 115–35.

A stimulating review of the literature, including many observations published since **O. W. Richards'** paper (1927, Biol. Rev. 2: 298–364). Appeals for further field-observations.

34. Edelsten, H. M. (1935). "The nuptial flight of *Hylesinus fraxini* Panz." Ent. Mon. Mag. 71: 259.

35. White, A. G. (1935). "*Hyloicus pinastri* and *Metopsilus porcellus*." Entomologist, 68: 218.

Female *H. pinastri* "asembling" male *M. porcellus*.

36. Benson, R. B. (1935). "Swarming of *Xyela julii* Bréb." Ent. Mon. Mag. 71: 245.

On birch catkins.

37. Fraenkel, G. (1935). "Observations and experiments on the blowfly (*Calliphora erythrocephala*) during the first day after emergence." Proc. Zool. Soc. Lond. 893–904.

The digging movements of freshly emerged *Calliphora* are found to be determined by light but not by gravity. The process of inflation of the fly with air, as well as the colouring and hardening of the skin are inhibited during the digging period.

38. Ratcliffe, F. N. (1935). "Observations on the sheep blowfly (*Lucilia sericata* Meig.) in Scotland." Ann. Appl. Biol. 22: 742–53.

After describing experiments to discover the number of eggs laid by females and the lengths of the larval, prepupal and pupal stages, detailed records of attacks ("strikes") in an Aberdeenshire flock throughout the 1933 and 1934 seasons are analysed. The figures agree with results obtained in other parts of Britain.

39. Mellor, J. E. M. (1935). "A fly developing at a constantly very low temperature." Ent. Mon. Mag. 71: 211.

The bluebottle, *Calliphora erythrocephala* emerged in a room of which the mean temperature was 5·02° C. (41·04° F.).

40. Frohawk, F. W. (1935). "*Macroglossum stellatarum* partiality to geraniums." Entomologist, 68: 288.

Sight attracts this moth, as well as the scent of the flowers.

41. Mellor, J. E. M. and **Woodman, R. M. (1935).** "A note on preliminary work on attractants for cabbage root fly (*Hylemyia* (*Chortophila*) *brassicae* Bché.) and carrot fly (*Psila rosae* L.)." Ent. Mon. Mag. 71: 258–9.

42. Edelsten, H. M. (1935). "The effect of the severe frost of 17th May on oak-feeding larvae." Proc. R. Ent. Soc. Lond. 10: 59–60.

10–15 degrees of frost were registered. The foliage of oak, ash, and beech was completely destroyed and as a result of the hot sun on the following day became hard and brittle. A week later numerous larvae (chiefly Tortricidae) were still alive, but showed signs of starvation. After a fortnight the new shoots were being gnawed by the larvae which had survived. Many general feeders left the oaks and fed on hazel, alder and birch. It is believed a great many larvae perished.

43. Morris, S. (1935). "*Euchloë cardamines*: three winters in pupal stage." Entomologist, 68: 163.

Further records of delayed emergence by **R. T. C. Lahey-Bean**, *ibid.* 164 (*Cucullia verbasci*); **B. H. Smith**, *ibid.* 188 (*Acosmetia caliginosa*); **G. E. L. Manley**, *ibid.* 204 (*Papilio machaon*).

44. Seabrook, W. P. (1935). "Crippled moths in 1935." Ent. Rec. 47: 130.

A large number of crippled moths were noted in 1935, presumably owing to the very cold spell in May.

45. Goffe, E. R. (1935). "Male Tabanidae (Dipt.) in the New Forest, Hants, 1933–34." J. Soc. British Ent. 1: 100–9.

Male Tabanidae are normally rarely seen and are distinctly rare in collections. After a long spell of hot dry weather they come to drink at the few places where water still remains and may be caught in large numbers. The author describes the capture of 303 males during the two exceptionally hot summers of 1933 and 1934 and gives details of their behaviour.

46. Mellanby, K. (1935). "The evaporation of water from insects." Biol. Rev. 10: 317–33.

A summary of this problem. Evaporation takes place through the spiracles, and when these are closed the air in the tracheae may become saturated. A saturation deficiency law is propounded which states that the rate of water loss from insects exposed to different humidities is proportional to the saturation deficiency.

47. Ramsay, J. A. (1935). "Methods of measuring the evaporation of water from animals." J. Exp. Biol. 12: 355–72.

Challenges the law of saturation deficiency on theoretical grounds as it suggests that the effect of temperature on gaseous diffusion is negligible.

48. Smart, J. (1935). "The effects of temperature and humidity on the cheese skipper *Piophila casei* (L.)." J. Exp. Biol. 12: 384–8.

Thermal death point of larva is found to be 52° C. for one hour's exposure and 45° C. for 24 hours. The point is lower for pupae and is shown to be due to a secondary physiological effect of the temperature.

49. Ramsay, J. A. (1935). "The evaporation of water from the cockroach." J. Exp. Biol. 12: 373–83.

Temperature, humidity and air movement are found to affect the tracheal evaporation of *Periplaneta americana* in a similar manner to a purely physical system. The process is complicated by the presence of a film of fatty substance which undergoes a change of state at about 30° C.

50. Baker, J. R. (1935). "Apparatus for measuring the drying power of the atmosphere." J. Sci. Instrum. 12: 214–16.

Description of apparatus for obtaining saturation deficiency from direct readings. This "xerometer" is a modified thermohygrograph made by Casella and Co. A "nomogram" is also described by means of which calculations can be made from the usual data.

51. Williams, C. B. and **Emery, G. A. (1935).** "A photographic moonlight recorder." J. Sci. Instrum. 12: 111–15.

Duration and intensity of moonlight are indicated by the darkening of a strip of photographic paper attached to a drum rotated by clockwork.

52. Löwenstein, O. (1935). "The respiratory rate of *Gammarus chevreuxi* in relation to differences in salinity." J. Exp. Biol. 12: 217–21.

Rate of respiration in this brackish water Amphipod was found to be midway between those of sea and fresh-water forms, and was 20 % lower in sea water than in the normal habitat (25 % sea water).

53. Moore, H. B. (1935). "The biology of *Balanus balanoides:* IV. Relations to environmental factors." J. Mar. Biol. Ass. U.K. 20: 279–307.

Barnacles found to be largest and most abundant in a wave-exposed locality at low water. In sheltered places the optimum level for growth, mean size, etc. is at low water for newly settled barnacles, but moves progressively up to high water as they grow older. Crowding reduces growth rate. Young barnacles orientate themselves with the current, adults across it. Inter relations with other organisms are discussed.

54. Lebour, M. V. (1935). "The breeding of *Littorina neritoides.*" J. Mar. Biol. Ass. U.K. 20: 373–8.

Combats the theory that molluscs living at or near high water tend to be viviparous or to have the veliger stage suppressed.

55. Russell, F. S. (1934). "The vertical distribution of marine macroplankton. XII: Some observations on the vertical distribution of *Calanus finmarchicus* in relation to light intensity." J. Mar. Biol. Ass. U.K. 19: 569–84.

Adults off Plymouth prefer higher intensities of light in July than they do in August. This change in habits coincides with a slight shift in average size.

56. Russell, F. S. (1935). "The seasonal abundance and distribution of the pelagic young of Teleostean fishes caught in the ring-trawl in offshore waters in the Plymouth area: Part II." J. Mar. Biol. Ass. U.K. 20: 147–79.

There is a gradual change, as the summer advances, from the young of northern to the young of southern species. From 1924–34 there were no signs of great fluctuations in numbers of small fish save for one instance each for mackerel and herring.

57. Cooper, L. H. N. (1935). "The rate of liberation of phosphate in sea water by the breakdown of plankton organisms." J. Mar. Biol. Ass. U.K. 20: 197–200.

Rate of breakdown of dead zooplankton was estimated by measuring the liberation of phosphates in laboratory experiments. Zooplankton breaks down more quickly than phytoplankton.

58. Keys, A., Christensen, E. H. and **Krogh, A.** (**1935**). "The organic metabolism of sea water with special reference to the ultimate food cycle in the sea." J. Mar. Biol. Ass. U.K. 20: 181–96.

Some quantitative experiments on the rate of bacterial development and oxygen consumption at the expense of dissolved organic nutriment in closed vessels of sea water.

59. Cooper, L. H. N. (**1935**). "A note on manganese in marine plankton." J. Mar. Biol. Ass. U.K. 20: 201–2.

Diatom collection found to have less than three parts per million million.

60. Lumby, J. R. (**1935**). "Salinity and temperature of the English Channel; estimation of mean values for the upper water layer over the 25-year period 1903 to 1927." Ministry Agr. Fish., Fish. Invest. Ser. 2, 14: No. 3, 1–67 (plus many tables). (London: H.M. Stationery Office. Price 7*s.*)

A thorough statistical analysis of the data, with monthly figures for 41 regions.

61. Carruthers, J. N. (**1935**). "The flow of water through the Straits of Dover, as gauged by continuous current-meter observations at the Varne Lightvessel (50° 56′ N.–1° 17′ E.). Part 2: Second report on results obtained." Ministry Agr. Fish., Fish. Invest. Ser. 2, 14: No. 4, 1–67. (London: H.M. Stationery Office. Price 3*s.*)

Records from a drift indicator at 6 fathoms during 1928–35. Wind direction and its relation to water movement are discussed. The flow is strongest in November and weakest in February. Its relations to winds and to the total volume of water in the North Sea are discussed.

4. PARASITES

See also **4, 10, 21, 38, 104, 105, 106, 107, 111, 119, 136**

62. Thompson, G. B. (**1935**). "The parasites of British birds and mammals. IV. Records of bat parasites." Ent. Mon. Mag. 71: 143–7.

63. Thompson, G. B. (**1935**). "The parasites of British birds and mammals. IV. Records of mammal parasites." Ent. Mon. Mag. 71: 214–19.

64. Radford, C. D. (**1934**). "Notes on mites of the genus *Myobia*." North Western Nat. 9: 356–64 and (**1935**) 10: 248–58.

Systematic account of a number of species with notes on their hosts (various mammals).

65. Boyd, A. W. (**1935**). "A fly parasitic on the swallow." British Birds, 28: 225.

Bluebottle larvae (*Protocalliphora caerulea*) parasitising young in nests in several places.

66. Donisthorpe, H. (**1935**). "Some parasites etc., in the nests of house martins (*Chelidon urbica*, Linn.) in Windsor Forest." Ent. Rec. 47: 130.

The bug, *Oeciacus hirundinis*; the fly, *Stenepteryx hirundinis*; the flea, *Ceratophyllus hirundinis*; a beetle larva, *Anthrenus* sp.; a spider, *Lycora amentata*.

67. Baylis, H. A. (**1935**). "Some parasitic worms from musk-rats in Great Britain." Ann. Mag. Nat. Hist. 15: 543–9.

Five species from England and Scotland, two being American forms.

68. Baylis, H. A. (**1935**). "Four new species of nematodes." Ann. Mag. Nat. Hist. 16: 370–82.

Includes *Metabronema truttae* from gut of brown trout in Wales.

69. Lebour, M. V. (1935). "*Hemiurus communis* in *Acartia*." J. Mar. Biol. Ass. U.K. 20: 371–2.

Nematodes within Copepods: unusual abundance of a usually rare phenomenon.

70. Thorpe, W. H. (1935). "The biology of *Encyrtus* (*Comys*) *infelix*, a remarkable Chalcid parasite of *Lecanium hemisphaericum*." Proc. R. Ent. Soc. Lond. 10: 62–3.

This Hymenopterous parasite attacks a common scale-insect pest in glassshouses. Its respiratory adaptations are of great interest as the chorion of the egg is prolonged to form a hollow stalk which projects through the skin of the host and enables the young larva to breathe atmospheric air while later the larva becomes invested with a membranous sheath which fuses with the tracheal system of the host so that the parasite is able to utilise the air contained therein.

71. Hey, G. L. (1935). "Notes on Tortricidae." Ent. Mon. Mag. 71: 253–5.

Deals with *Batodes angustiorana* Haw. and lists *Apanteles longicaudis* Wesm., *Apanteles* sp., *Macrocentrus abdominalis* Fab. and *Actia pilipennis* Fln. as larval parasites.

72. Hey, G. L. (1935). "A list of parasites bred from *Tortrix* and Tineid hosts." Ent. Mon. Mag. 71: 186–7.

73. Hamilton, A. G. (1935). "Miscellaneous observations on the biology of *Apanteles glomeratus* L. (Braconidae)." Ent. Mon. Mag. 71: 262–70; and (**1936**) 72: 24–7.

5. FOOD AND FOOD HABITS

See also **88, 92, 98, 111**

74. Spooner, G. M. and **Moore, H. B. (1935).** "Oyster catchers and limpets." British Birds, 29: 90.

Broken shells of *Patella vulgata* suggest that the oyster catcher eats limpets, though this was not actually observed.

75. Campbell, J. W. (1935). "Shore birds and molluscs." British Birds, 29: 183.

Various molluscs found in stomachs of shore feeding waders.

76. White, C. M. N. (1935). "Meadow-pipits eating the 'magpie moth', *Abraxas grossulariata* L." Proc. R. Ent. Soc. Lond. 10: 80–1.

The magpie moth is a typical example of a distasteful species, but so-called inedibility is entirely relative to the presence of other more palatable food. On this occasion the magpie moths were "incredibly numerous". Comments on the above note also include an account of the larvae of this moth being eaten by cuckoos while they were avoided by other birds.

77. Parmenter, L. (1935). "Diptera as food of starling and rock-pipit." British Birds, 29: 113.

Several actual records, giving species (*Borborus* and *Bibio*).

78. Brindley, M. D. (1935). "The female pied wagtail feeding her brood on dragonflies, on the Cam, at Cambridge, July 1935." Proc. R. Ent. Soc. Lond. 10: 64–5.

On two out of four visits she carried at least one of the slender blue dragonflies, probably *Calopteryx virgo*.

79. Hodgson, S. B. (1935). "Lepidoptera eaten by bats and birds." Entomologist, 68: 286.

80. Frohawk, F. W. (1935). "Feeding butterflies in captivity." Entomologist, 68: 164.

Instances of keeping species of butterflies alive for a longer period than their natural lives by feeding on sugar and water. *Maniola jurtina* survived 44 days, *Callophrys rubi* 6 weeks, *Nymphalis antiopa* 3 months.

Further reference by **C. Nicholson**, *ibid.* 188.

81. Buckstone, A. A. W. (1935). "Food-plant of *Hipocrita jacobaeae*." Entomologist, 68: 188.

Feeding on groundsel (*Senecio vulgaris*) in Surrey, and not on the ragwort (*S. jacobaea*) in an adjacent meadow.

82. Dannreuther, T. (1935). "Note on the food-plant of *Danaus plexippus*, L." Entomologist, 68: 240–1.

83. Cockayne, E. A. (1935). "Additional food-plants of the larva of *Parascotia fuliginaria*, L." Ent. Rec. 47: 91.

Circumstantial evidence, confirmed by behaviour in captivity, that the caterpillars of this moth had been feeding on the fungus *Daldinia concentrica*.

84. Taher el Sayed, M. (1935). "On the biology of *Araecerus fasciculatus* de Geer (Col., Anthribidae), with special reference to the effects of variations in the nature and water content of the food." Ann. Appl. Biol. 22: 557–77.

60 % R.H. is about the limit at which the life cycle can be carried on with maize and nutmeg, 80 % R.H. for cacao, at 27° C.

85. Lowndes, A. G. (1935). "The swimming and feeding of certain Calanoid Copepods." Proc. Zool. Soc. Lond. 687–715.

The females of *Euchaeta norvegica* are said to feed almost entirely on *Calanus finmarchicus*. The feeding of these Copepods is to some extent selective.

86. Harvey, H. W., Cooper, L. H. N., Lebour, M. V. and **Russell, F. S. (1935).** "Plankton production and its control." M. Mar. Biol. Ass. U.K. 20: 407–41.

A study of relations between phyto- and zooplankton to find effects of "grazing". It is concluded that grazing does have an appreciable effect on phytoplankton production.

6. ANIMAL POPULATIONS

See also **42, 44, 69, 86, 129, 140**

87. Anon. (1935). "Musk-rats in Scotland." Scottish J. Agric. 18: 175–8.

The numbers had been reduced to a very low level, and musk-rat family life thought to be broken up.

88. Ticehurst, C. B. (1935). "On the food of the barn-owl and its bearing on barn-owl population." Ibis, 5: 329–35.

Analysis of pellets from several counties of England. The author speculates on the probable density of small mammals necessary to support a pair of owls on a given area. On the basis of observations in Kent (where one pair ate on the average 8·6 animals per night, i.e. 3139 per year) and assuming that 5 pairs of owls live on 1 square mile (Blaker's highest figure) every 100 square yards would have to provide very many more than two animals (the number actually eaten is estimated at half an animal per night on every 100 square yards).

89. Huxley, J. and **Nicholson, E. M. (1935).** "The bird population of Britain: a plea for co-operative study." Geogr. Mag. 2: 39–52.

An excellently illustrated general account of bird population work that is being done in Great Britain, with special reference to the British Trust for Ornithology.

90. Wild, S. V. (1935). "A local bird census." North Western Nat. 111–17.

A census based on 56 visits during 1933, on an arable and meadow area partly encroached upon by suburbs, near Timperley and Brooklands Stations, Manchester. 26 species were noted, and the numbers in different months are listed in detail. Densities are not given.

91. Nicholson, E. M. (1935). "The index of heron population, 1935." British Birds, 29: 98–101.

Figures and a map of a sample heron census of England and Wales in 1935, compared with previous years. The total number of breeding pairs was slightly below that in 1934. North, west, midland and south-east regions showed a general increase since 1928, balanced by decrease in the east, Thames basin, and south-west.

92. Middleton, A. D. (1935). "Factors controlling the population of the partridge (*Perdix perdix*) in Great Britain." Proc. Zool. Soc. Lond. 795–815.

Gives field observations and statistics on the mortality of partridges on game preserves at various stages from egg to adult. The average losses on sample estates were 22 % of nests, 7 % of eggs incubated unhatched, 52 % chick mortality, 55 % of survivors shot, and 40 % winter "disappearance". A technique has been evolved for measuring the population annually, based largely on sample counts in summer showing the surviving proportion of young and old, combined with nest censuses, clutch counts, etc.

93. Gordon, S. (1936). "The fulmar petrel." Nature, 137: 173–6.

A summary of some recent records of the spread of the fulmar round the shores of the British Isles.

94. Price, M. P. (1935). "Notes on population problems and territorial habits of chiff-chaffs and willow-warblers." British Birds, 29: 158–66.

Census of total numbers of adults, nests, unmated cocks, and broods reared, on 2000 acres in 1934 and 1935, with data for a smaller area covering 9 years. In both species 40–60 % of the cocks were unmated. Detailed notes on habitats.

95. Price, M. P. (1935). "Census of nightingales in Gloucestershire." British Birds, 29: 81–3.

The population on a sample area of 2000 acres in 1935 was approximately double that of previous 3 years. Of 27 adults on 7000 acres, 7 were unmated males with song territories. **G. E. Took** (*ibid.* 29: 121) states that on an area in Kent only 1 out of 19 birds was an unmated male.

96. Emmet, H. J. (1935). "Swallow clutches and broods." British Birds, 29: 149–50.

5 pairs raised 35 young from 45 eggs in 10 nests (including second nests) in Sussex, 1935.

97. Mackworth-Praed, C. W. and **Gilbert, H. A. (1935).** "The Orielton Decoy—past and present." British Birds, 29: 167–71.

Extracts from records since 1877 of various species of ducks caught in and visiting a decoy lake in Wales.

98. Serle, W. Jnr. (1935). "Mortality amongst young red-throated divers." British Birds, 29: 181–2.

None of 11 pairs observed managed to rear two young from their two eggs. Black-headed gulls suspected of killing the young.

99. Greenwell, J. (1935). "Weardale kingfishers." Vasculum, 21: 121–7.

Descriptive account of this species in the Bishop Auckland district where it is fairly common. "It would appear that the kingfisher is becoming more widely diffused, or attracting more attention."

100. McWilliam, J. M. (1935). "Roosts of twites in Outer Hebrides." British Birds, 29: 78.

Estimated 100–200 twites roosting in willow plantation in North Uist, Outer Hebrides, July 1935.

101. Ross, W. M. (1935). "Some incubation- and fledging-periods." British Birds, 29: 111.

Crested tit, goldcrest, sedge-warbler, robin, and common wren.

102. Mountfort, G. R. (1935). "Variations in the weights of birds." British Birds, 29: 145–8.

213 individuals of 22 species weighed at a ringing station in France.

103. Temperley, M. A. (1935). "Longevity of frogs." Vasculum, 21: 110–11.

Frogs in garden were probably at least 8 years old.

104. Anon. (1935). "Salmon and freshwater fisheries: Report for the year 1934." Ministry Agr. Fish., Fisheries—England and Wales, pp. 1–37. (London: H.M. Stationery Office. Price 1*s*.)

Statistics of catches of salmon and trout in various districts. Drought affected fish in various ways, and the season was not a very good one. The remarks are, however, of too general a nature to give a very clear picture of what happened during the year to the fish populations. Furunculosis was widespread but not severe, except in the Wye. Trout, chub, and grayling also had this disease locally. There is a brief survey of the river pollution question, and of special measures and experiments in connection with it, also notes on ecological investigations in progress at Alresford.

105. Powell, T. P. P. and **Phillips. F. A. (1935).** "Wye Board of Conservators: Annual Report, Season 1934." (Hereford.)

The Wye (as shown by the Ministry of Agriculture and Fisheries figures) had in 1933 the highest rod catch in England and Wales, but was eighth in order of net catches. The rod catch in 1934 was slightly higher than in 1933 but not so high as the peak year 1932. The grilse run was the highest for at least 20 years, probably as a result of the good smolt migration of 1933. About 21 tons of salmon were netted in the estuarial waters. Details of age-classes (by weight), spawning, etc. are given. There was disease, partly furunculosis, especially in July.

106. Powell, T. P. P. and **Phillips, F. A. (1936).** "Wye Board of Conservators: Annual Report, Season 1935." (Hereford.)

The rod catch this year was very high, being close to that of 1927. The grilse run was lower than in 1934. Big fish were also less abundant. About 27 tons were caught in the estuarial waters of the district. Good spawning season. There was a fairly serious outbreak of furunculosis.

107. Adamson, W. and **Buxton, N. (1935).** "Final Report (July 1935) of the Furunculosis Committee appointed July 1929, pp. 1–67. (Edinburgh: H.M. Stationery Office. Price 2*s*. 6*d*.)

Furunculosis has spread to 6 new districts in the last 2 years. 31 areas in England and Wales and 28 in Scotland are now infected. Migratory Salmonidae become infected in fresh water. A bacteriophage is at times associated with the disease. In the summer of 1933 experiments were conducted by Isobel Blake and others at Edinburgh University in a tank holding 200 fish. An epizootic was produced in one-third of the population through contact with 10 fish inoculated with *B. salmonicida*. Mortality reached its height in 4–9 days and continued intermittently until

checked by low autumn temperatures (50° F.). Occasional deaths occurred in winter, especially among fish weakened by spawning. Epizootics developed spontaneously in spring at a minimum temperature of 50° F. and optimum of 55–66° F. Disease is maintained up to 4 months in a few carriers of the "incubationary" type. Bacilli are located in the kidney.

108. Nall, G. H. (1935). "Sea-trout of the Montrose District. Part 2: Growth on the scales of recaptured fish." Fisheries, Scotland, Salmon Fish. 1935: No. 2, 1–22. (Edinburgh: H.M. Stationery Office. Price 2*s*.)

With certain exceptions, the validity of the principle of scale interpretation was confirmed through a study of the scales of marked fish recaptured after known intervals of time.

109. Macfarlane, P. R. C. (1934). "Salmon of the River Tay, 1930." Fisheries, Scotland, Salmon Fish. 1934: No. 5, 1–20. (Edinburgh: H.M. Stationery Office. Price 1*s*. 3*d*.)

Details of the composition of the 1930 catch from a study of scales. There was an increase in grilse numbers.

110. Davis, F. M. and **Buchanan-Wollaston, H. J. (1934).** "Mesh experiments with trawls, 1928–33." Ministry Agr. Fish., Fish. Invest. Ser. 2, 14: No. 1, 1–56. (London: H.M. Stationery Office. Price 2*s*. 6*d*.)

Problem: how to spare undersized fish through the use of large mesh. A "codend" was covered with a bag of fine-mesh, the end of which could be closed off to separate the fish released during the two operations: towing and hauling. The proportion released during towing is extremely high. Normal and large-meshed gear was used alternatively by two sister ships fishing under similar conditions. The large mesh caused no financial loss and brought up less rubbish. The investigation also covers other types of saving gear and various methods of investigating the size of fish released by codends.

111. Cameron, E. (1935). "A study of the natural control of ragwort (*Senecio jacobaea* L.)." J. Ecol. 23: 265–322.

A very comprehensive and important study, fully illustrated, of the ecology of ragwort, with special reference to possible controlling animals required for introduction into New Zealand. Includes a useful summary of other weed control research. Ragwort was introduced into New Zealand before 1874: it causes damage as a weed and by poisoning stock, especially horses and cattle. The two main possible controlling insects are the moth, *Tyria jacobaeae*, and the Anthomyiid fly, *Pegohylemyia seneciella*. The ecology of these is fully analysed, with special reference to parasites. Rabbits and sheep are also important factors in control. Fungi also have some effect. There is high mortality in the pupae of the moth in this country, thought to be due to moles. Insects and other animals do not control ragwort except on poor soils, as the plant may have a second flowering after attack. It is likely that grazing policies can be altered so as to discourage ragwort, which establishes best in open soil conditions, and not so easily in closed turf.

112. Donisthorpe, H. (1935). "Abundance of *Lucanus cervus*, L., in Windsor Forest." Ent. Rec. 47: 104.

This stag-beetle occurred by hundreds in 1935; whereas in all the years the author has explored the Forest he has only previously encountered this species four or five times and always singly.

113. Donisthorpe, H. (1935). "Two other insects in great profusion." Ent. Rec. 47: 104.

The beetle, *Stenus picipes*, and the fly, *Sepsis cynipsea*.

114. Latter, O. H. (1935). "Unusual length of life and curious site of larva of *Cossus ligniperda*." Proc. R. Ent. Soc. Lond. 10: 41.

A full-grown caterpillar of the goat-moth found in a floor-board of a house; it seems probable that the larval period of this specimen lasted about 7 years.

115. Head, H. W. (1935). "Where do 'Red Admirals' go to in the winter in England?" Entomologist, 68: 213–14.

Further note by **K. M. Hinchliff**, *ibid.* 282.

116. Newcombe, C. L. (1936). "Validity of concentric rings of *Mya arenaria* L. for determining age." Nature, 137: 191–2.

For certain areas at any rate (in this case Bay of Fundy, Canada) the rings give a safe index of age, as proved by field planting experiments with this bivalve.

117. Wright, F. S. (1935). "Report on investigations into the condition of certain of the oyster beds in the South Wales Sea Fisheries District (June, 1934)." Ministry Agr. Fish., Fish. Invest. Ser. 2, 14: No. 5, 1–29. (London: H.M. Stationery Office. Price 2*s.*)

Surveys were done in Swansea Bay and Milford Haven to find the state of the oyster beds which had seriously declined about 1922. Some beds were found in 1934 to be carrying a moderate stock with only a small mortality. Oyster populations apparently depend (like beech trees) on recurrent heavy spat years, of which there were about 17 in the years 1846–1900 in the Essex and Kent area. A useful table of good and bad spat years in different areas is given, and limited data for South Wales. The causes of the fluctuations discussed.

118. Moore, H. B. (1934). "The biology of *Balanus balanoides*: I. Growth rate and its relation to size, season, and tidal level." J. Mar. Biol. Ass. U.K. 19: 851–68.

The growth rate varies with age (more rapid at first), season, and tidal level, but in general there is a maximum growth period in summer and minimum in winter. They grow fastest high up on the shore, except during the first year. Most lower and middle zone barnacles die in their third year, but those in the extreme top zone may live 5 years or more.

119. Marshall, S. M., Nicholls, A. G. and **Orr, A. P. (1934).** "On the biology of *Calanus finmarchicus*: V. Seasonal distribution, size, weight, and chemical composition in Loch Striven in 1933, and their relation to the phytoplankton." J. Mar. Biol. Ass. U.K. 19: 793–827.

Includes also some notes on parasites and on diatom fluctuations.

120. Hardy, A. C. (1935). "The continuous plankton recorder: a new method of survey." Rapp. Cons. Explor. Mer. 95: 36–47.

The recorder is towed behind ships across the North Sea. Bolting cloth passes across a water tunnel, filters the plankton and is wound into a tank of formalin. Counts of the number of organisms per division of cloth and hence per mile of ocean give a measure of seasonal and local variations. Diagrams illustrating a number of North Sea transects are given.

7. MIGRATION, DISPERSAL, AND INTRODUCTIONS

See also **20, 26, 31, 34, 35, 82, 115**

121. Anon. (1935). "Recovery of marked birds." British Birds, 28: 235–40 and 261–8.

Detailed records of recoveries of birds ringed in the British Isles.

122. Witherby, H. F. and **Leach, E. P. (1935).** "Movements of ringed birds from abroad to the British Isles and from the British Isles abroad." British Birds, 29: 132–44.

Records of all recoveries notified in 1935.

123. Witherby, H. F. and others (1935). "Immigration of crossbills." British Birds, 29: 112–13, 148–9, 175–6, 214–15.

Reports from many observers indicated small numbers widely scattered, but no big immigration, in 1935.

124. Portal, M. (1935). "Large movements of jays in Hampshire." British Birds, 29: 174–5.

Flocks migrating in September and October 1935. The numbers, direction and dates are given. **H. F. Witherby** (*ibid.* 29: 212–14) gives more information on this movement.

125. Craster, J. M. (1935). "Inland occurrence of sea-birds." Vasculum, 21: 107.

Arctic tern, 2½ miles from sea; fulmar, 5 miles from sea.

126. Hartley, P. H. T. (1935). "A contribution to the study of sea-bird movements." British Birds, 29: 203–10.

There was increase in general movement, especially among shearwaters, gannets and auks, in high wind and stormy weather. Details are given of birds moving off the Cornish coast in spring and summer 1932–5.

127. Lockley, R. M. (1935). "Movements of Manx shearwaters." British Birds, 29: 105–7.

Some ringed on Skokholm, South Wales, and recovered up to 600 miles south, in the Bay of Biscay, in April are thought to be non-breeders.

128. Nall, G. H. (1935). "Sea-trout of the Montrose District. Part 3: The migrations of sea-trout." Fisheries, Scotland, Salmon Fish. 1935: No. 3, 1–24. (Edinburgh: H.M. Stationery Office. Price 2*s.*)

Gives a summary of all previous recaptures of fish marked by the Board and details of movements of fish marked at three centres in 1933–4. Most recaptures have been in or near the river in which the fish were marked, but this is partly due to greater difficulty of capturing sea-trout at sea. The longest journeys recorded were 100 miles (3 cases), 125, 175, and 300 miles.

129. Nall, G. H. (1935). "The sea trout of Mull." Fisheries, Scotland, Salmon Fish. 1935: No. 1, 1–44. (Edinburgh: H.M. Stationery Office. Price 2*s.* 6*d.*)

Scale and size measurements from 11 centres showed the age at which different stages in the life history occur. Most of the smolts migrate after 2 years in the rivers.

130. Dannreuther, T. (1935). "Migration records, 1935." Entomologist, 68: 161–2.

Further references in *ibid.*, 185–8, 209–12, 252–9; and, by **F. W. Frohawk**, 262 and 285–6.

131. Whitehouse, B. (1935). "Further migration records for 1934." Entomologist, 68: 147.

132. Nicholson, C. (1935). "*Danaus plexippus* L. in the British Isles." Entomologist, 68: 245–51, 269–73.

Complete list of the recorded appearances of this butterfly since 1876.

133. Anon. (1935). "Emigration of *Plusia gamma*." Ent. Rec. 47: 102–3.

Thousands of specimens of this moth coming from the north and proceeding out to sea on August 4, 1935, at the Start Lighthouse.

134. Williams, C. B. (1935). "A mass flight of the cabbage white fly (*Aleurodes brassicae*)." Entomologist, 68: 218–19.

In November at Harpenden.

135. Turpin, S. J. (1935). "A daylight flight of Corixidae." Ent. Mon. Mag. 71: 259.

They flew only in sunshine, then dived into water. Migration of these water bugs has been stated to take place only at night.

136. Davies, W. M. and Whitehead, T. (1935). "Studies on aphides infesting the potato crop. IV. Notes on the migration and condition of alate *Myzus persicae* Sulz." Ann. Appl. Biol. 22: 549–56.

Migrating alatae are the main source of the initial infestation of *M. persicae* on the potato crop, but the introduction of virus diseases into a healthy stock by such forms is slight compared with that spread subsequently by the apterous aphids moving within the crop.

137. Thompson, G. B. (1935). "(I) Two further records of the association of Hippoboscidae and Mallophaga. (II) An Anthocorid bug feeding on *Dermanyssus gallinae* (Redi)." Ent. Mon. Mag. 71: 162–3.

138. Crawford, G. I. (1935). "*Corophium curvispinum* G. O. Sars, var. *devium* Wundsch. in England." Nature, 136: 685.

This Amphipod was found in mud tubes made among submerged plants in the River Avon at Tewkesbury, in June 1935. It is known to live in rivers entering the Caspian, Black Sea, Baltic and parts of the North Sea, but not west of the Elbe. It has been spreading in Germany. It is a fresh-water variety of a species found in the Caspian Sea. It is not known how it reached England.

139. Beauchamp, R. S. A. (1935). "The rate of movement of *Planaria alpina*." J. Exp. Biol. 12: 271–85.

The rate of movement of this Planarian appears to be, except at temperatures below 2° C., a direct function of heat.

140. Gardiner, A. G. (1934). "Variations in the amount of macroplankton by day and night." J. Mar. Biol. Ass. U.K. 19: 559–67.

The more common species of macroplankton off Liverpool, Nova Scotia, were found in May to appear in greater numbers at night than during the day: among these were *Thysanoessa raschii*, *T. inermis*, *Sagitta elegans*, *Calanus hyperboreus*, and *C. finmarchicus*. Adults of the last species tended to be absent in the day more than did the stage 5 young.

8. BIBLIOGRAPHY

141. Hobby, B. M. (1935). "A bibliography of entomological notes and papers contained in the serial publications issued by local scientific societies in the British Isles. Part III." Trans. Soc. British Ent. 2: 167–233.

This part deals with *The Naturalist*, and covers the period 1864–1930. The entries are classified into orders and arranged alphabetically by authors. They deal largely with the entomology of the north of England, especially that of Yorkshire.

BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING (UNIVERSITY OF READING) JANUARY 3RD–5TH, 1936

THE twenty-third annual meeting of the Society began on the afternoon of January 3, the President, Prof. MATTHEWS, in the Chair.

Mr H. BAKER gave an account of a three years' study of seasonal variation in *p*H values of the soils of Bagley Wood, near Oxford. The results mainly concerned analyses made over a period of three years upon four types of woodland soil overlying respectively plateau gravel, sand, clay and clay loam. In all the soils there was a marked change of acidity with depth; in the sands and clays the subsoil was less acid but there was a reversal of the normal gradient in the clay loams. The most striking feature of the results was, however, a very marked tendency to a seasonal periodicity in acidity, expressed as a late summer maximum and a winter or early spring minimum, the bottom soils having a marked lag in this rhythm as compared with the upper soils. Mr Baker showed that rainfall seemed to have a considerable effect on the seasonal curve, disturbing the regularity of the rhythm. In the discussion which followed Dr Godwin, Prof. Tansley, Dr Clapham, Prof. Matthews and Dr Turrill took part and the hope was strongly expressed that Mr Baker would extend his studies for a further period of years, especially since the weather of 1933 and 1934 was decidedly abnormal.

Mr Ross read a paper on the regeneration of tropical rain-forest at a site 100 miles east-north-east of Lagos in Southern Nigeria. The characters of the undisturbed rain-forest and of the clearings made by the natives for cultivation were illustrated by very beautiful photographs taken on the Cambridge Botanical Expedition to Nigeria. Mr Ross then gave a detailed account of investigations on the vegetational processes following abandonment of such clearings after four or five years' occupation. Vegetational analyses showed a rapid colonisation by (1) weeds of cultivated land, (2) plants peculiar to secondary forest, and (3) seedlings of primary forest trees. In the second class the most permanent species was *Musanga smithii* (Musaceae), which became an early dominant in the secondary colonisation, reaching a height of 40 ft. at 6 years, but dying out, presumably through senescence, at about 50 years, when it had reached a height of 70 or 80 ft. Mr Ross showed that in all probability primary forest was rapidly re-established as a result of this secondary succession. In the discussion which followed Mr Gilmour, Prof. Tansley, Mr Fishlock, Dr Godwin and Mr Milne-Redhead took part.

Mr WILKINS gave an account of investigations carried out under his direction on the ecology of the larger fungi in various types of woodland near Haslemere in Surrey. Over a period of several years oakwoods, beechwoods, grassland, open heath and *Calluna* heath had been examined, but the larger number of examples were concerned with the oak and beechwoods. It appeared from the examination of fourteen beechwoods and eleven oakwoods that there was a greater constancy in the fungal species in individual oakwoods than in individual beechwoods, that the species of high constancy were mostly common ones, and that only a very few were exclusive species. At the same time, the common species varied much in constancy in the two types of woodland. Thus, for example, *Mycena pelianthina* was chiefly in the beechwoods, *M. polygramma* was common in oak and not in beech, *M. pura* was found only in beechwoods, and *M. sanguinolenta* was common in both. In conclusion, Mr Wilkins discussed the best methods of estimating the fungal flora of woods and many of the questions which followed turned on this point. Prof. Matthews and

Prof. Tansley, Dr Somerville Hastings, Dr Burtt Davy, Dr Clapham, Mr Baker and Dr Watson took part in the discussion which followed.

Exhibits in the Department of Botany

After tea in the University Common Room members visited the exhibits set out in the Botanical Department.

Dr Watson showed a number of lichens taken from the bark of oaks in *Quercus sessiliflora* woods growing on carboniferous limestone at Killarney, including *Parmelia atlantica*, a species newly created by Degelius.

Dr Ingold had set out a series of rare fungi found in the neighbourhood of Reading, and specimens of the orchid, *Epipogum aphyllum*, which is also found locally.

Dr R. W. Butcher showed a series of herbarium specimens of water buttercups grown under varying experimental conditions: these included forms of *Ranunculus peltatus* with elongate peduncles, which have hitherto been described as varieties.

Prof. Harris showed an exhibit illustrating the effect of adding large amounts of nutrient to algal cultures. This treatment caused the disappearance of nearly all animals and filamentous algae, but the Protococcales increased enormously and were represented by about twenty species, many quite uncommon in Britain.

Dr Hubbard set out a series of microscopic and herbarium preparations to illustrate the contrast in structure between tropical and temperate grasses. Tropical savanna grasses are characterised by a chlorenchyma closely set round the vascular bundles, whilst in many temperate grasses the chlorenchyma is evenly distributed through the mesophyll. Dr Hubbard demonstrated that this structural difference could be recognised in tropical grasses naturalised in the British Isles, such as species of *Cynodon*, *Panicum*, etc., and he illustrated the value of the character as a taxonomic criterion.

Mr Ballard showed some extremely interesting specimens of various members of the Cyperaceae, Velloziaceae and Gramineae, which have evolved a curious pseudodendroid habit, apparently in association with a rocky habitat and a long rainless period. *Microdracoides squamosus*, a native of West Africa, was perhaps the most striking of these species. The vertical rhizome, clothed by descending roots, progressively dies from the base although the plant itself continues living at the apex of this dead column of tissue.

Mr Ross showed a series of photographs taken on the Cambridge Botanical Expedition to Nigeria illustrating the structure of primary and secondary rain-forest.

Dr Godwin set out a series of pollen analysis diagrams from the Fenland showing the appearance of the beech and hornbeam in greater or less amount in the upper peat layers from several sites. It appeared from these results that the beech was present in East Anglia in pre-Roman times and probably began to increase in numbers in the late Bronze Age.

Members and guests were entertained in the evening at a *soirée* held in Wantage Hall. About fifty members and guests were present.

The annual meeting was resumed on the morning of January 4 at 10 a.m., about fifty members being present. Apologies for absence were read from Dr Gurney, Mr Oldham and Dr Pearsall.

The minutes of the last general meeting were read and confirmed.

The following new members were elected: Miss Waloff, Miss Eyre, Mr Plomley, Mr Mohr and Mr Horne.

The Treasurer reported on the finances of the Society and presented provisional accounts and balance sheet. He announced a deficit on the year's working. Prof. Tansley proposed the adoption of the accounts subject to correction and audit and this was approved

unanimously. Dr Watson proposed that Messrs William Norman and Son be reappointed auditors to the Society for 1936. A very hearty vote of thanks to Mr Boyd Watt for his valuable services as Treasurer was moved by Prof. Tansley and carried *nem. con.* It was proposed from the Chair and adopted *nem. con.* that the yearly grant of £5 for the transplant experiments of the Society be renewed for 1936. The Honorary Secretary's report on the work of the past year was read and adopted.

Hon. Secretary's Report for the year 1935

The twenty-first annual meeting of the Society was held in the Department of Botany, University College, London, on Saturday, January 5, 1935. A *soirée* was given on the evening before the meeting, and a large number of exhibits was on view, for the most part illustrative of ecological work carried out by research students and staff of the Department. A large number of members and guests were present at the *soirée*, and the sincere thanks of the Society are given to Prof. Salisbury for having organised it and for having again given generous facilities for meeting in his Department.

After careful consideration by the Council it was decided to accept the kind invitation of Prof. Hardy and Mr D'Oyly Good to hold a summer meeting of the Society under their joint leadership at Hull. It was fixed for August 28–31, 1935, and a programme of wide interest was arranged and circulated to members. The notifications of intention to attend were, however, so few that the meeting had to be cancelled. It seems probable that a major cause of the failure was the very intensive programme of excursions and meetings available to British botanists during the summer: at the same time there was equally little response from animal ecologists although many features intended to be of special interest to them had been arranged. The Society owes thanks to Dr Hardy and Mr Good for the considerable trouble they spent, and regrets that it should have been to no purpose. The Council would welcome more guidance and support from members in the arrangement of the summer meetings.

On Saturday, October 19, a joint excursion with the British Mycological Society was held at Box Hill under the leadership of Mr J. Ramsbottom. It was well attended.

In the past year two numbers of vol. IV of *The Journal of Animal Ecology* have been published, appearing in May and November. They contained respectively 165 and 172 pages, a considerable advance in size on the earlier volumes. In all twenty-nine original papers were published, with nine plates, in addition to notes, notices and reviews. Notices of publications on Animal Ecology have been continued, and in this volume totalled 226 classified entries.

Since the last annual meeting there have been issued two numbers of vol. XXIII of *The Journal of Ecology*, appearing in February and August and containing respectively 264 and 289 pages, with thirty-eight plates. In this volume have been published twenty-two original papers, besides book reviews and notices.

Mr Marsden Jones and Dr Turrill report continued satisfactory progress with the Society's transplant experiments at Potterne.

Since the last annual meeting the membership of the Society has risen from 331 to 341: there have been twenty-three new members elected, and thirteen members have resigned or died. Of the present membership list, 188 members receive *The Journal of Ecology*, 101 *The Journal of Animal Ecology* alone, 49 receive both Journals, and 3 neither. These figures include elections made at the General Meeting.

The Secretary then asked for the advice of the meeting on the question of the time and place of the summer excursion for 1936, and outlined the chief features of two alternatives, namely the Lake District and south-western Ireland. After some discussion it appeared that there was a general feeling in favour of the Irish excursion.

REVENUE ACCOUNT FOR YEAR ENDING 31ST DECEMBER, 1935

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears	472	7	10			
Less Prepayments for 1936–9	22	0	0			
	450	7	10			
Less Transferred to *Journal of Animal Ecology* (see below)	177	12	6			
				272	15	4
Interest on Investments	34	10	0			
Interest on Deposit Account	1	5	2			
				35	15	2
Journal of Ecology—Sales, etc.:						
Current volume, XXIII, 1935	461	0	8			
Back volumes and parts	27	14	4			
				488	15	0
Index Volume, *Journal of Ecology* (vols. I–XX), Sales				6	3	4
Journal of Animal Ecology—Sales, etc.:						
Vol. IV, 1935: Subscriptions received	177	12	6			
Sales	167	16	4			
Sales of reprints	40	5	6			
Vols. I–III: Sales of back numbers	54	18	3			
				440	12	7
				1244	1	5
Balance, Deficit for the Year				96	12	6
				£1340	13	11

Expenditure

	£	s.	d.	£	s.	d.
Working Expenses:						
Printing Circulars, etc.	2	0	6			
Postages, etc.	8	4	11			
Bank Charges		4	5			
Clerical assistance (Secretary and Treasurer) ...	15	0	0			
				25	9	10
Soirée Expenses				7	2	4
Audit Fee				3	3	0
Grants:						
Fresh water Biological Association of the British Empire				10	0	0
B.E.S. Transplant Experiments Fund				5	0	0
Journal of Ecology, vol. XXIII (1935):						
Paper, Printing, Illustrations, etc.	680	2	0			
Binding	4	1	0			
Publishers' Commission	72	15	6			
Carriage and Postages, Insurance, etc.	46	0	5			
Copies bought in	23	8	0			
				826	6	11
Index Volume, *Journal of Ecology*, vols. I–XX:						
Sundry Expenses				1	4	2
Journal of Animal Ecology, vol. IV (1935):						
Paper, Printing, Illustrations, etc.	404	13	11			
Publishers' Commission	36	17	6			
Carriage, Insurance, Advertising, etc.	20	16	3			
				462	7	8
				£1340	13	11

BALANCE SHEET AT 31ST DECEMBER, 1935

Liabilities

	£	s.	d.	£	s.	d.
Membership Subscriptions, prepaid for 1936, etc....				22	0	0
Journal of Animal Ecology, vol. IV, pt. 2:						
Printing Account due	187	1	10			
Less Sale of reprints	6	7	0			
				180	14	10
Library Account				1	5	0
General Revenue Account—Balance of Funds:						
Balance at 31st December, 1934	993	7	6			
Less Deficit at 31st December, 1935	96	12	6			
				896	15	0
				£1100	14	10

Assets

	£	s.	d.	£	s.	d.
Westminster Bank– Credit Balances:						
Current Account	73	16	10			
Deposit Account	100	0	0			
				173	16	10
Sundry Debtors:						
Subscriptions due				11	5	0
Investments:						
£700 3½ % War Loan at cost (Market value at 31st December, 1935, at 106, £742)	717	3	0			
£200 5 % Conversion Loan at cost (Market value at 31st December, 1935, at 120, £240) ...	198	10	0			
				915	13	0
				£1100	14	10

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates.

(Signed) WM NORMAN & SONS,
Chartered Accountants.

120, BISHOPSGATE, LONDON, E.C. 2.
20th January, 1936.

NOTE. A further asset is the unsold stock of the *Journals* and Index Volume held for the Society by the Publishers.

(Signed) HUGH BOYD WATT,
Hon. Treasurer.

The Council proceeded to the election of officers and the following were elected.

President: Dr W. H. Pearsall.
Vice-President: Prof. E. J. Salisbury, F.R.S.
Hon. Editor Journal of Ecology: Prof. A. G. Tansley, F.R.S.
Hon. Editor Journal of Animal Ecology: Mr C. S. Elton.
Hon. Secretary: Dr H. Godwin.
Ordinary Members of Council: (in place of Mr E. Price Evans and Prof. Salisbury) Prof. A. C. Hardy, Dr W. Leach.

In the absence of the new President and Vice-President Prof. Matthews was asked to continue in the Chair.

The revised constitution and rules of the Society as circulated beforehand to members were then discussed and unanimously adopted subject to a minor alteration proposed by Dr Watson and accepted *nem. con.* (see pp. 220–2).

At the conclusion of the business meeting Prof. T. A. Stephenson gave an account of the ecology of the intertidal region of the South African coast with special reference to the habits of limpets. The coastal fauna and flora of the Cape differs very sharply on the eastern and western coasts on account of the warm Agulhas current on the one side and the South Atlantic up-welling of polar water on the other. One method of attack on the problems of faunal distribution consisted in the examination of the behaviour of eleven species of limpet (*Patella*). An extremely interesting account was given of the breeding, zonation, geographical distribution and habits of these animals, and it was evident that a very close relationship existed between their method of life and their position on the shore. A great deal of interest centred in the feeding habits of such species as *P. granularis*, which feeds in the dark when the waves have retreated, leaving its scar on the rock, and browsing some distance away, to return directly to the same scar again with the rising tide. The wandering habit was more marked in the forms occupying upper littoral zones. In one species, *P. cochlea*, a grazed fringe of the red alga *Gelidium* was constantly associated with each limpet and various suggestions were put forward to explain the association. A very long and interesting discussion followed in which Dr Clapham, Prof. Tansley, Prof. Matthews, Prof. Weiss, Dr Ashby, Dr Watson, Mr Price Evans, Dr Burtt Davy and Dr Godwin took part.

Dr A. R. Clapham gave a concise statement of his views on the use of quantitative data on the distribution of individual plants and their statistical treatment in the study of vegetation. In briefly adverting to the history of the subject he suggested that statistical methods had been employed to elucidate (*a*) the space relations of individuals of one species, or the relations of one species to another; (*b*) the changes in distribution of species with time; and (*c*) in the definition and diagnosis of plant communities. He suggested that the methods were likely to be of use for purposes (*a*) and (*b*) rather than for (*c*), and explained a method of determining the dispersion of members of a species and expressing it in terms of "relative variance":

$$\frac{V}{m} = \frac{S_1^n (x-m)^2}{(n-1)_m}.$$

V/m is greater than unity in cases of over-dispersion (i.e. aggregation in patches) and is less than unity in under-dispersion (i.e. spacing more even than random spacing). He gave examples to show that there is a substantial change in the relative variance of species at different stages of a plant succession, and discussed cases in which the application of this method should prove useful. Prof. Tansley and Mr Valentine asked questions of the speaker, and Dr Ashby then gave an account of an alternative method, developed with Mr Stevens, of discovering the degree of under- or over-dispersion of individual species. This was based on random casts of a grid containing sixteen or twenty-five equal squares,

and the scoring of the number of individuals and the number of empty squares found within the grid. He quoted examples from open Salicornietum on salt-marsh, from regenerating birchwood and from abandoned arable ground on chalk downs. He also concluded that there was no valid method at present available for using statistics in the classification of vegetation and agreed that these methods should be applied to the examination of the distribution of individual species. In the following discussion Dr Godwin, Dr Turner, Dr Clapham, Dr Butcher and Mr Ross took part.

The meeting was adjourned for lunch in the Common Room and was resumed in the afternoon.

Prof. ADAMSON gave an account of a new classification of South African vegetation types. He emphasised the dependence of the vegetation on climate which was itself much influenced by topography, causing in particular a very striking change in the rainfall from east to west. The South African forests are very limited in extent and are little studied: they are mainly evergreen and show a striking absence of dominants. Four types are distinguishable, the subtropical rain-forest of the eastern coast, a small-leaved forest (Knysna type) of the southern coast allied to the sclerophyll bush of the Cape and in which *Olea* and *Podocarpus* are abundant, a more deciduous type in Natal and the south-east of the Cape Province and evergreen forest on higher mountains in a region of very heavy rainfall and mostly at about 5000–6000 ft. The rest of the country he separated into sclerophyll bushland, semi-desert with a rainfall below 12 in. and open vegetation with no dominants, savanna, bush veldt and grassland. He suggested that the grassland is separable from savanna by the much greater temperature extremes, particularly by frost making tree growth impossible: and the semi-desert region was subdivided on a basis of these temperature fluctuations, those parts with the greatest extremes having an open vegetation with dry scrub, the intermediate having succulents of the *Mesembryanthemum* type and those where frost is absent having succulents of large size. In the discussion which followed Prof. Tansley, Dr Burtt Davy and Dr Godwin took part.

Prof. TANSLEY gave an account of experiments suggested by himself and carried out by Mr Baker and Dr Clapham on the early growth of *Quercus robur* and *Q. sessiliflora*. After a brief account of the climatic and soil preferences of the mature trees as usually understood, Prof. Tansley described experiments in which seeds of both species were sown in pots containing woodland soils of acidity varying from *p*H 3·6 to 8. There was exactly similar germination in both species and the soils showed no differential effect, but *Q. robur* grew taller in all soils, and the height growth of both species was greater on the more acid soils. The two species differed in the earlier emergence and growth of primary root and shoot in *Q. sessiliflora*, in the greater rate of growth of *Q. robur* in later stages, in the earlier slowing off of height growth in *Q. sessiliflora* correlated with the earlier date at which leaves of this species reached full size. A second series of experiments involving waterlogging of pot cultures showed that *Q. robur* suffers more severely than *sessiliflora*, though both are severely affected by complete waterlogging.

In the very interesting discussion which followed, Dr Watson, Dr Godwin, Dr Thomas, Mr Gilmour, Mr Ross, Prof. Matthews and Mr Baker took part.

The meeting closed with the proposal by Prof. Weiss on behalf of the Society of a very hearty vote of thanks to the University authorities for their kind hospitality in giving the use of the University buildings and of Wantage Hall to the Society for the meeting, and to Professor and Mrs Harris for the kindness they had shown in entertaining us. This was carried with acclamation.

Excursion to Beech Woods

Owing to the unfortunate absence through indisposition of both Dr Watt and Mr Harley the proposed excursion to the Beech Woods of the Chiltern Hills had to be abandoned and an alternative shorter excursion was arranged under the leadership of Prof. Harris and

Dr Somerville Hastings. The party first visited, in the neighbourhood of Peppard Common, a small area of acidic heath formed on gravel over chalk and bearing characteristic vegetation with *Ulex minor, U. europaeus, Calluna* and *Pteridium*. On the other side of the valley there was an extremely characteristic area of chalk scrub showing abundant tree invasion by beech, ash, oak, holly, yew and elm. The party then proceeded to the main objective of the excursion, namely beech woods growing on chalk or on drift overlying chalk. Over large parts the beech had been exploited by selective cutting at a diameter of 6–8 in., the wood being used for the local manufacture of chair legs and brush backs, etc. The beech reaches a height of 55–60 ft. and *Fraxinus* and *Quercus robur* occur frequently, especially in the areas where cutting has taken place. Ground vegetation is generally sparse, though *Corylus, Sambucus, Daphne laureola, Prunus cerasus* occur locally and *Ilex* is often extremely abundant, spreading by suckers forming large thickets. The holly appears to be subject to the severe attack of rodents, most probably rabbits. The Society is much indebted to Prof. Harris and Dr Somerville Hastings for having organised such a satisfactory excursion on the spur of the moment.

THE BRITISH ECOLOGICAL SOCIETY

FOUNDED 1913

CONSTITUTION AND RULES

(*Revised formulation adopted by the Society on January 4th*, 1936)

1. The object of the BRITISH ECOLOGICAL SOCIETY shall be to promote and foster the study of Ecology in its widest sense.

2. The Society shall consist of Ordinary Members, Hon. Members and Associates as defined in these rules.

3. Applicants for Membership of the Society shall be proposed by one Member (from personal knowledge) or by an Officer of the Society (not necessarily with personal knowledge) and seconded by one or more other Members. Such applications shall be made on a form to be supplied by the Hon. Secretary, and duly filled up and signed by the applicant.

Election shall take place either at a General Meeting or at other times by resolution of the Council. A majority of votes in favour shall result in the election of the applicant.

The Secretary may, however, be empowered by the Council to circulate the names of applicants for membership to members of Council by post, and if he receives no intimation of objection within one week, the applicant shall be deemed to be elected.

4. Subscriptions shall be payable in advance and shall be due on January 1st each year. The minimum Annual Subscription for Ordinary Membership shall be twenty-five shillings (25*s*.) and for Associate Membership seven shillings and sixpence (7*s*. 6*d*.). Members who pay a yearly subscription of 25*s*. shall have the right to receive post free **either** *The Journal of Ecology* **or** *The Journal of Animal Ecology*. An Annual Subscription of 45*s*. shall entitle Members to receive post free **both** of the Journals above named.

5. In addition to receiving one or both of the Journals of the Society, ordinary members shall have the following privileges:

(*a*) To receive on application any other publications of the Society free or at a reduced rate, as the Council may from time to time determine.

(*b*) To have the use on loan, under regulations, of any photographs or lantern slides in the Society's collections, and of books, maps and pamphlets in the Society's Library.

(*c*) To vote in the election of Council and of Officers.

(*d*) To be eligible for service on the Council and its Committees, or as Officers.

6. Associate Members shall have the right to attend Meetings and Excursions, to obtain through the Secretary such advice and assistance as the Society can afford, to have the use of photographs and the Library, but they shall not have the privileges of Ordinary Members indicated in 5 (*c*) and 5 (*d*).

7. Local Natural History Societies may at the discretion of the Council be allowed to subscribe to the Society not less than twenty-five shillings (25*s*.) per annum and shall thereby be entitled to receive a copy of **either** of the two Journals of the Society, or on payment of forty-five shillings (45*s*.) per annum, to receive **both** Journals of the Society. In either case they shall also be entitled (*a*) to such advice or assistance as the Society can afford, and (*b*) to send two delegates to the Society's Meetings, to have the same privileges as Associate Members as regards such Meetings.

8. The Society shall be governed by a Council of fifteen Members consisting of the Officers of the Society, namely, the President, two Vice-Presidents, the two Hon. Editors, the Hon. Secretary and the Hon. Treasurer, together with as many ordinary members of Council as may be needed to raise the total to fifteen.

Officers and ordinary members of Council shall be elected at the Annual Meeting of the Society.

9. Each ordinary member of Council shall be elected for a period of four years, at the end of which time he shall retire. He shall not be eligible for re-election until the Annual Meeting of the year following that of his retirement.

An ordinary member of Council when elected an Officer of the Society shall cease to be an ordinary Council Member: on expiry of office the retiring President, Hon. Secretary, Hon. Treasurer and Hon. Editors shall be eligible for immediate re-election as ordinary members of Council, and the retiring Vice-President shall complete his term of four years' service on the Council.

10. The President and the two Vice-Presidents shall be nominated from among the Members of Council. The two Hon. Editors and the Hon. Secretary shall retire at the end of each year but shall be eligible for immediate re-election.

11. The President of the Society shall hold office for two years, and it shall be his duty to deliver an address to the Society at the Annual Meeting next after that at which he was elected.

12. One Vice-President shall be appointed each year and shall hold office for two years.

13. The Hon. Treasurer shall hold office for three years and shall be eligible for re-election. The Treasurer shall keep the Society's funds. His sanction shall be required for the disbursement of the Society's moneys and he shall present a financial statement at the Annual Meeting. The financial status and policy of the Society shall be considered each year at a meeting of the Council held as soon as practicable after the audit. The audited accounts shall be published in the Journals of the Society.

14. The Hon. Secretary shall be responsible for collection of subscriptions.

15. If any Council Member does not attend at least one meeting of the Council during the year he shall retire at the end of the year, but shall be eligible for re-election.

16. At least one fortnight before the Annual Meeting the Secretary shall circulate to all Members of the Society a list of the Members of Council including Officers, indicating those who retire and adding the names of nominees of the Council to fill the vacancies.

17. Members may propose for ballot at the Annual Meeting the name or names of any duly qualified Member or Members in place of any or all of the Council's nominees.

18. The Council shall have power to co-opt any ordinary Member of the Society to fill vacancies occurring during the year among Council or Officers, the tenure of such co-opted Members to terminate at the next Annual Meeting.

19. At the Annual Meeting, after nomination by the Council, persons who have rendered conspicuous service to the subject of Ecology may be elected Honorary Members of the Society.

Such Hon. Members shall receive free either or both Journals of the Society as the Council may determine, and shall also have the other privileges of ordinary members of the Society.

20. The Annual Meeting shall be held in December or in the following January. At least one other Meeting shall be held later in the year. Further Meetings and Excursions may be held at such times and places as the Council may from time to time determine.

21. At the Annual Meeting the Members of the Society present shall elect the Officers and Council, in the case of a contested election by ballot, and consider any other business brought before them by the Council; or business brought before them by any Member, of which four weeks' notice in writing has been given to the Secretary.

22. Alterations of the Rules shall only be made at the Annual Meeting and require six weeks' notice in writing to the Secretary and a majority of two-thirds of the Members voting.

23. Members desiring to present communications at any Meeting must give due notice to the Secretary, stating the nature of the communication and the time required.

24. At any Meeting of the Society the Chairman shall decide as to procedure and the order of business. It shall be within the Chairman's discretion to admit communications or other business, other than alterations to the Rules, not included in the programme.

25. A Meeting of the Council to consider the Annual Report shall be held shortly before the Annual Meeting.

26. The Society shall issue two Journals, *The Journal of Ecology*, and *The Journal of Animal Ecology*.

27. The subscription price of each Journal to others than Members of the Society shall be as determined by the Council.

28. No Member shall be entitled to receive the Journals of the Society whilst his subscription is in arrear.

(This revised formulation of the constitution and rules was accepted at the Annual Meeting of the Society, January 4th, 1936.)

LIST OF MEMBERS (January 6th, 1936)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, Dr H. Godwin, Botany School, Cambridge.

E. A. **Adams**, Dr Charles C.; New York State Museum, Albany, N.Y., U.S.A.
E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
A. **Alexander**, W. B., M.A.; University Museum, Oxford.
E. **Allan**, Dr H. H.; Plant Research Institute, Palmerston North, N.Z.
A. **Allee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
E. **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
E. **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
E. **Alvarez-Laviada**, Prof. M. M.; Estación Navanjerade Levante, Burjasot (Valencia), Spain.
E. **Anand**, P. L., M.Sc.; c/o Messrs Grindlay and Co., 54, Parliament Street, London.
E. **Andersonian Naturalists' Society** (cf. Glasgow).
E. A. **Arkwright**, J. A., M.D., F.R.S.; Lister Institute, Chelsea, London, S.W. 1.
E. **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
E. **Ashby**, Eric, B.Sc.; The University, Bristol.
E. **Bacon**, Mrs Alice; The Technical College, Brighton.
E. **Ballard**, F., B.Sc.; The Herbarium, Royal Botanic Gardens, Kew.
A. **Barber**, Miss E. G.; Harborne, Westbourne Avenue, Emsworth, Hants.
E. **Barnes**, Dr B.; 28, Torridon Road, London, S.E. 6.
A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
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